THE STRUCTURE AND REPRODUCTION OF THE ALGAE

VOLUME I

BY

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PREFACE TO VOLUME I

At the present time of great activity in botanical research, when communications to be reckoned by their thousands are appearing yearly in a steadily increasing number of periodicals, no apology is needed for an attempt to bring together what is known and to survey the momentary position that has been reached in one branch of the subject. There has never been a comprehensive account of the morphology of the Algae in the English language, in fact prior to Oltmanns' epoch-making work nothing of the kind was available, and one has only to realise the immense stimulation which the publication of his book gave to research on algal morphology to justify the attempt to produce something analogous in English. Although I have devoted most of my scientific life to algal investigation, there are many aspects of the study of Algae into which I have never entered save as an interested spectator. My interest has, however, been sufficiently alive to make me feel at home in most branches of algology, and I believe that I shall not be accused of undue temerity in attempting to give an account of the whole group.

The two volumes in which I propose to accomplish this task are planned to deal essentially with morphological features, and points relating to the physiology and ecology of the Algae have been included only where their consideration appeared relevant to an understanding of the main subject-matter. Nor is this in any sense a taxonomic work. The outlines of classification given under the individual groups are intended merely to afford a synopsis for the reader, and taxonomic problems have only been discussed where they are of general morphological interest. Some attempt has been made, without entering into detail, to deal with the numerous cytological papers that have been published during the present century, but this has certainly been the hardest part of my task. There is often little agreement among investigators and in some cases a mere citation of the relevant literature seemed to be the best method of treatment. Many of the discrepancies are probably due to lack of uniformity of material and to examination of a form at different stages of its life-history. To my thinking every one attempting a cytological investigation should first become fully acquainted with the Alga in a living condition.

This work is designed as an introduction to the study of the Algae in the widest sense and with this object in view I have included all the holophytic Protista, as well as their immediate non-holophytic allies. The reasons that justify this mode of treatment are given in full in the introductory pages to this volume. I have aimed at a broad treatment of the subject-matter, such as will give a general review of the characteristics and interrelationships of the diverse groups of Protista and will furnish a groundwork upon which further detailed knowledge can be acquired by a consultation of the literature. It is hoped in this way to provide a basis for the prosecution of research, the more as great care has been expended on the citation of literature. The lists have been compiled on the principle of citing all the literature published since 1890,[1] with the omission only of certain papers that did not appear to be of material importance from the point of view of the subject-matter. Prior to 1890 in general only the more fundamental memoirs on which the modern superstructure rests have been included. This involves the omission of a considerable number that were important in their day, but are now no longer directly relevant. Even with their exclusion the literature bulks largely and, although this has the unfortunate consequence of appreciably increasing the size and cost of the book, it would not fulfil its proper function if such detailed lists were omitted. All the references have been personally checked with the exception of a few which, even with the splendid facilities afforded by the London libraries, could not be examined. In such cases the source of the reference is stated.

I cannot fail to pay a tribute to the immense help afforded by Oltmanns' *Morphologie und Biologie der Algen*, without the existence of which the labour of compiling such a book as this would have been appreciably greater. Much help has also been obtained from the general sections of Pascher's *Süsswasserflora*, the *Natürliche Pflanzenfamilien* and certain volumes of Rabenhorst's *Kryptogamenflora*. The literature affords such a wealth of excellent illustrations that little attempt has been made to provide new figures; in every case the author of the figure is mentioned under its description. Special acknowledgments for permission to reproduce figures are due to Messrs Gustav Fischer, Jena, for figs. 5 B; 51 F; 111 C; 117 G, L, N; 120 A and B; 123 B–D, H, I; 127 G; 134 D–F, L–N from Oltmanns' *Morphologie*

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[1] The literature is dealt with up to the end of , although a few papers that appeared after that date have been included. All papers are cited by number only and are arranged alphabetically at the end of each section, except for a few that came to my notice too late to be included in the correct sequence; these are listed at the end of each of the respective bibliographies.

und Biologie der Algen; for figs. 210O, Q and 244R taken from Belar's *Der Formwechsel der Protistenkerne*; and for figs. 3F; 6A; 154B–D; 187F, K; 191A; 192B, E, F; 194A, G, H; 195A–C, K; 200K; 201H; 216I, K, L taken from Pascher's *Süsswasserflora*; also to the Akademische Verlagsgesellschaft, Leipzig, for figs. 185; 187A; 201I; 223H; 224F taken from Rabenhorst's *Kryptogamenflora*. I am also indebted to my friend Prof. A. Pascher of the University of Prague for the drawings of *Tetragonidium* in fig. 219, to Mr G. J. Hollenberg of Stanford University, California, for those of *Halicystis* in fig. 116, and to Dr M. A. Pocock for those illustrating the germination of the oospore of *Volvox* (fig. 28L–Q). Miss F. Rich, M.A., has very kindly drawn figs. 57A, B and fig. 123F. My especial thanks are due to Mr R. Cullen, Laboratory Steward in the Department of Botany, Queen Mary College, who has spared no pains to make the photographic reproduction of the numerous figures taken from other sources as clear as possible. I also owe a debt of gratitude to the staff of the University Press for the care that has been bestowed on the printing of the book.

F. E. FRITSCH

INTRODUCTION

ALGAE AND FLAGELLATA

It will be generally familiar that, apart from the very frequent occurrence of motile reproductive cells (zoospores, gametes) in the life-cycles of many Algae, there exists a large number ot forms—many of them unicellular (e.g. *Chlamydomonas*, fig. 1 C)—in which the ordinary individuals exhibit active movement also throughout a great part of their vegetative existence. While motile reproductive stages are almost invariably naked, the cells of the independent free-moving unicellular and colonial types are either naked or provided with a definite membrane similar to that present in most non-motile (sedentary) forms. In the past organisms possessing such cell-walls (e.g. Volvocales), in so far as their cells were provided with chromatophores, have by botanists been classed among the Algae, whilst the naked forms have been referred to the Flagellata, regarded by zoologists as a group of the Protozoa. Additional characteristics of these Flagellata were thought to be the occurrence of division in the longitudinal plane only, the almost invariable absence of sexual reproduction, and the ready adoption of a resting stage accompanied by the secretion of a thick enveloping membrane (cyst-formation) (cf. (7), (87) p. 278).

To the Flagellata were also referred many colourless types, some of which have proved to be very closely related to the pigmented forms and have no doubt originated from the latter by loss of the photosynthetic pigments (cf. especially pp. 90, 538), and this is possibly true of a far larger number than is at present apparent. Many of these colourless Flagellata are saprophytes, whilst others exhibit holozoic nutrition (i.e. ingestion of solid food), but this animal characteristic is occasionally met with also in the pigmented (holophytic) types or even in evident Algae according to the older definition (133).

Klebs (88), as long ago as 1893, drew attention to the affinity between the pigmented Flagellata and the Algae, and during the present century the distinctions that were formerly used to separate these two sets of organisms have broken down utterly. With the marked advancement of our knowledge within the last decades it has become clearly apparent that forms with an altogether similar habit may in one class exhibit algal characteristics (possession of a cell-wall, sexuality, etc.) and in another flagellate characteristics (cf. (49) and (132)). Thus, the majority of the motile unicells among the Chlorophyceae (Isokontae) are on the older definition Algae, while the equivalent forms among Xanthophyceae (Heterokontae) and Chrysophyceae are Flagellata, and the same fact emerges if one compares other types of habit found in the different classes. It is therefore unwise to place any considerable stress on the differences between algal and flagellate organisation. The algal characteristic of possessing a cell-wall is one which probably appeared at different stages in the evolution of the various classes of Protophyta, and we shall certainly not go far wrong if, for instance, we regard the bulk of the Chlamydomonadineae from a comparative standpoint as scarcely less primitive than the Chrysomonadineae. True, in the latter sexuality appears to be lacking or to be of rare occurrence, but that is equally true of some classes of undoubted Algae (Myxophyceae). Moreover, sexuality has proved to be more widely distributed among flagellate forms than was at first thought to be the case. Nor is longitudinal division in any way purely a characteristic of the so-called Flagellata, since it is recognisable in many algal types and even in advanced forms (140).

It will be clear, therefore, that the old distinction between Algae and Flagellata can no longer be maintained. This has long been recognised in the case of the Xanthophyceae (Heterokontae), but is equally applicable in all other cases. It may in fact be doubted whether, from the point of view of the botanist, the designation Flagellata should not be altogether abandoned (cf. (49)),[1] since its retention tends to introduce confusion into a clear concept of the Protophyta. Much that is especially instructive from the standpoint of comparative evolution is obscured or even lost sight of, as long as Algae and Flagellata are regarded as something different.

Unless purely artificial limits are drawn, the designation alga must include all holophytic organisms (as well as their numerous colourless derivatives) that fail to reach the higher level of differentiation characteristic of the archegoniate plants. The latter can be clearly demarcated only on the basis of the greater specialisation attained by their reproductive organs and of the stereotyped nature of their life-history, for the alga may show a morphological elaboration and an anatomical differentiation that is quite equivalent to or even exceeds that found in many Bryophyta. Except for the antheridium of Charales,[2] however, the reproductive organs of the Algae never possess a cellular wall that plays no part in the formation of the reproductive cells.

The essentially negative nature of the definition of the Algae given

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[1] The zoologist, in view of the marked holozoic tendencies evident especially in certain series of these forms, will no doubt continue to include them among the Protozoa and will retain the name Flagellata for them. There is nothing to be said against this, provided the plant-like characteristics are clearly emphasised. By comparison with the other groups of Protozoa the Flagellata appear primitive.

[2] Even here the structure is open to another interpretation, cf. p. 459.

in the first sentence of the preceding paragraph is due to the enormous range in structure, reproduction, and life-history which they exhibit. They include at the same time the simplest unicellular forms of holophytic plants, as well as elaborate multicellular organisms displaying a considerable measure of division of labour. The reproductive processes comprise the most primitive known methods of propagation, but at the other extreme, among the advanced forms, attain to a degree of complexity that falls little short of that of the higher types of plants. The life-cycle shows almost every conceivable variant.

There are few[1] nowadays who doubt that an early phase in the evolution of the simpler pigmented Protophyta was in all cases a unicellular, uninucleate organism provided with special photosynthetic pigments lodged in more or less sharply differentiated parts of the cytoplasm, the *chromatophores*, and in many cases sooner or later acquiring special propelling organs in the shape of complex prolongations of the cytoplasm, the *flagella*. It is possible that in some classes (Rhodophyceae, Myxophyceae) flagella were never acquired and that motility was lacking even in the ancestry, but a large number of the present-day classes of Protophyta include such free-moving unicellular organisms. We may justly see in them a semblance of what the early forms of Protophyta were like. Moreover, we are warranted in regarding the fundamental differences that they exhibit among one another as illustrative of diverse evolutionary trends that originated during the early beginnings of life, how and from what ancestry we know not.[2] The description and classification of the innumerable types of motile unicells is still in its beginnings and new forms are constantly being discovered, but it is already clear that there are many different series. These are distinguished by the number and mode of arrangement of the flagella, the nature of the pigments contained in the chromatophores, the forms in which the products of photosynthesis are stored up in the cells, and by other less constant and therefore less important features. In many series at least the differences appear to be largely of a physiological nature.

Among the colonial and cellular Algae there are some which exhibit not only the same pigments in the chromatophores and the same photosynthetic products as are found in certain series of motile unicells, but their motile reproductive cells (swarmers) exhibit the same number and orientation of the flagella. Compare, for instance, the zoospores of *Enteromorpha* (fig. 1 B) or *Tetraspora* (fig. 30 E, p. 123) with the individuals of a *Carteria* (fig. 12 A, B, p. 82) or *Chlamydomonas* (fig. 1 C); or the swarmer of a *Chrysosphaera* (fig. 1 M) with a *Chromulina* (fig. 1 J). Resemblances of this kind were

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[1] Cf. however (119*a*), (170*a*).

[2] Church (21–23) has developed a number of ingenuous hypotheses as to the mode of origin of these early types.

matters of frequent comment in the past, but it was not until nearly the end of the last century that the full conclusion was drawn from them and the doctrine of the origin of most classes of the Algae from motile unicellular forms clearly expounded. Every class of Protophyta was conceived as beginning with unicellular types of a distinctive kind. It thus became apparent, thanks to the researches of Borzi (12), Luther (103), and Bohlin (9), that the Green Algae included members of two totally distinct series (Isokontae and Heterokontae) sharply distinguished from one another by the essential characteristics above mentioned (see also p. 5). In both these series more or less simple unicellular types and more elaborate, multicellular, "algal" forms were represented. There still remained, however, a multiplicity of groups of motile unicells of which no higher "algal" members were known, and alternatively there were such large classes as the Phaeophyceae and Rhodophyceae of which no certain, primitively unicellular representatives had been discovered.

The second half of this statement is still true at the present day,[1] but the investigations of Klebs (90), Pascher (132, 141, 142), and Conrad (25) have shown that in a number of groups until recently deemed purely "flagellate" (e.g. Chrysomonadineae, Peridinieae), more or less numerous forms with "algal" organisation also exist. It is possible that in the future all the old flagellate groups will be shown to comprise some representatives with an "algal" organisation. Whether that proves to be the case or not, we are justified in giving them equal status with the groups in which evolution of such forms has been established. As a matter of fact there are only two such groups at present clearly distinguishable, the Chloromonadineae and the Euglenineae, the latter being so specialised in certain directions that the finding of "algal" representatives is perhaps improbable.

As regards the algal classes in which no flagellate members are known, they afford sufficiently clear evidence of a separate ancestry, either in the possession of swarmers of a distinctive type (Phaeophyceae) or, where these are lacking, in the presence of special pigments and photosynthetic products (Rhodophyceae, Myxophyceae) or other peculiar features (Bacillariophyceae).

THE BROAD CLASSIFICATION OF THE ALGAE

On the basis of the previous considerations it is possible at the present day to distinguish clearly eleven classes of the Algae. The brief characterisation of each given below will be sufficient to indicate the

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[1] Some of the Bangiales (Rhodophyceae) are unicellular, but it is probable that these are reduced forms (cf. vol. II). Pascher (*Rep. of Proc. 5th Internat. Bot. Congr.* Cambridge, 1930 (1931), p. 320) has referred to the existence of simple Phaeophyceae, but none such have so far been described.

essential differences between them, but much is of necessity omitted and a proper familiarity with each class is only to be obtained by a study of its chief members. The termination "phyceae" has been adopted wherever the class includes forms with an algal organisation, whilst for those few in which none such are known the old flagellate designation is retained.

The eleven classes are as follows:

I. *Chlorophyceae* (*Isokontae*),[1] with chromatophores which are grass green and contain the same four pigments (two green, two yellow) and approximately in the same proportions as in higher plants. Starch is the customary form of storage of the products of photosynthesis, often (especially in resting stages) accompanied by oil, and pyrenoids commonly surrounded by a starch-sheath (fig. 1 A, B, *p*) are frequently present in the chromatophores (chloroplasts). The algal members have a cell-wall in which cellulose is often a prominent constituent. The motile cells (fig. 1 B, C) exhibit the same features and possess a number of equal flagella (commonly two or four) which arise from the front end of the swarmers and are all similarly orientated. In many members the cells contain only one or few chromatophores. The majority of the members are algal and many exhibit sexuality (ranging from isogamy to advanced oogamy, usually with retention of the ovum). The highest type of structure attained is that of the heterotrichous filament (p. 20) and bulky parenchymatous forms are not realised, although the Siphonales show types of thallus-construction parallel to those found in Brown and Red Algae. The majority of the Chlorophyceae are haploid with the zygote representing the only diploid phase, but some exhibit a regular alternation of similar haploid and diploid individuals; the Siphonales are probably in the main diploid. The class is more widely represented in fresh than in salt water, and there is a marked terrestrial tendency.

II. *Xanthophyceae* (*Heterokontae*),[2] with chromatophores which are yellow-green owing to the presence of an excess of the yellow xanthophyll. Starch is absent and pyrenoids are wanting or rarely evident, oil being the customary storage-product (fig. 1 D, *o*). The algal members have a cell-wall which is often rich in pectic compounds and which is frequently composed of two equal or unequal pieces overlapping at their edges (fig. 1 E, F). Resting stages with a silicified membrane are of common occurrence. The motile cells (fig. 1 D, G, H) possess two very unequal flagella (or sometimes only one) arising from the front end. As a general rule the cells contain a number of discoid chromatophores (fig. 1 G–I). The majority of the members are algal, but sexual reproduction is rare and always isogamous. The most advanced forms have a simple filamentous habit. All are probably haploid. The class is more widely distributed in freshwater than in the sea.

III. *Chrysophyceae*, with brown or orange-coloured chromatophores containing one or more accessory pigments (phycochrysin). Starch is

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[1] See also p. 60.

[2] See also p. 470.

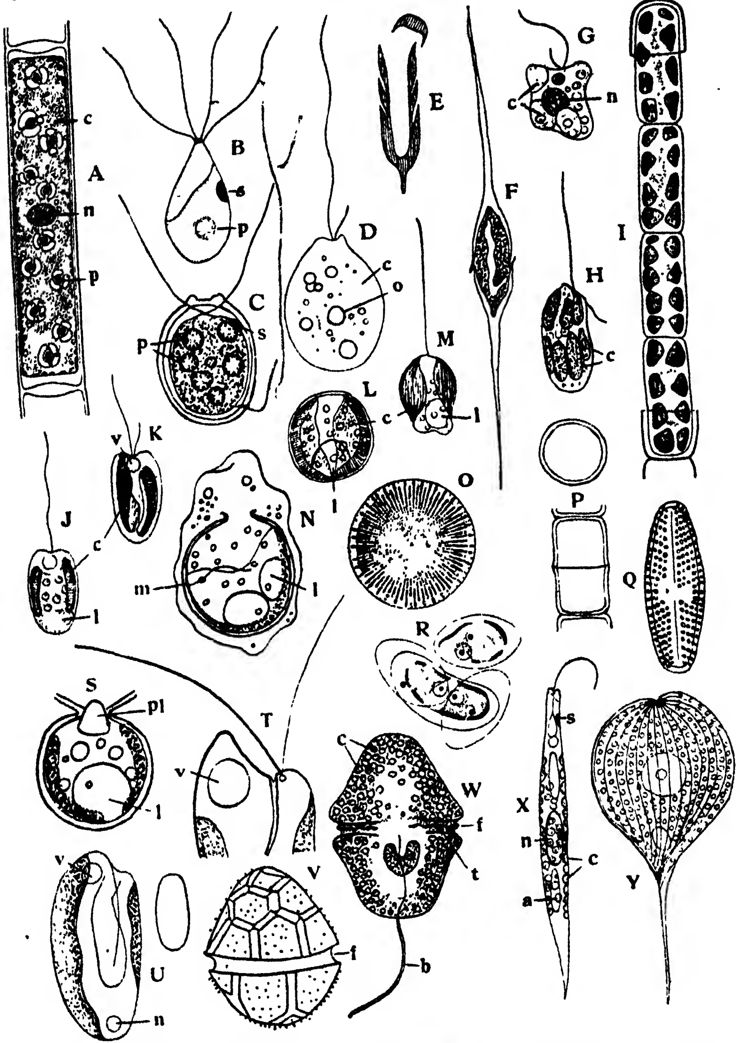

Fig. 1. Essential characteristics of the classes of the Algae. A–C, Chlorophyceae. A, cell of *Mougeotia* (after Palla); B, zoospore of *Enteromorpha* (after Kylin); C, *Chlamydomonas* (after Fritsch & Takeda). D–I, Xanthophyceae. D, *Chloromeson* (after Pascher); E, *Ophiocytium*, membrane-structure (after Bohlin); F, *Centritractus* (after Schmidle); G, *Chloramoeba* (after Bohlin); H, zoospore of *Tribonema* (after Luther); I, *Bumilleria*, part of thread (after Borzi). J–N and S, Chrysophyceae. J, *Chromulina* (after Klebs);

absent, but naked pyrenoid-like bodies are occasionally present; fat and a compound leucosin, occurring in the form of rounded whitish opaque lumps (fig. 1 L, M, *l*), are the customary forms of food-storage. A large proportion of the members are flagellate and devoid of a special cell-membrane. A marked characteristic is constituted by the spherical silicified cysts which arise endogenously (fig. 1 N) and are usually provided with a relatively small aperture closed by a special plug (fig. 1 S, *pl*). The motile cells (fig. 1 J, K, M) possess one or two (rarely three) flagella attached at the front end; in one series the flagella are unequal. The cells typically contain one or two parietal chromatophores (fig. 1 J–M, *c*). Holozoic nutrition is not infrequent. The most advanced habit is that of a branched filament. Sexual reproduction is extremely rare and not yet quite clearly established in any one case; the existing records point only to isogamy. The class is widely distributed in colder freshwaters, but a few families are marine.

IV. *Bacillariophyceae* (Diatoms), with yellow or golden brown chromatophores containing, apart from the usual ones, accessory brown pigments of disputed nature. Bodies like pyrenoids are often present and the products of photosynthesis are fat and volutin. All the members are unicellular or colonial. A cell-wall is always present and is composed partly of pectic substances and partly of silica; it invariably consists of two halves, each composed of two or more pieces and is commonly richly ornamented (fig. 1 O, Q). One set of forms (Centrales) is radially (fig. 1 O, P), the other (Pennales) bilaterally symmetrical (fig. 1 Q). The occurrence of flagellate stages is highly probable in Centrales, but still awaits a full elucidation. The Diatoms are a highly differentiated group, the Pennales showing a special type of sexual fusion between the protoplasts of the ordinary individuals (fig. 1 R). The members of this class are probably all diploid. Diatoms are very widely distributed in the sea and in all kinds of freshwaters, as well as in the soil and in other terrestrial habitats.

V. *Cryptophyceae*, with usually two large parietal chromatophores (fig. 1 U) showing very diverse pigmentation (commonly some shade of brown). Pyrenoid-like bodies occur, but appear often to be independent of the chromatophores; the products of photosynthesis are

K, *Ochromonas* (after Pascher); L, vegetative cell and M, swarmer of *Chrysosphaera* (after Pascher); N, stage in cyst-formation and S, fully developed cyst (after Pascher). O–R, Bacillariophyceae. O, *Coscinodiscus* (centric) and P, *Melosira* (centric, filamentous) (after West); Q, *Navicula mutica* (pennate) (after Bristol); R, sexual fusion in *Cocconeis* (after Geitler). T, U, Cryptophyceae. T, anterior end of *Cryptochrysis* and U, cell of *Cryptomonas* (transverse section at right) (after Pascher). V, W, Dinophyceae. V, *Peridinium* (after West); W, *Glenodinium* (after Schilling). X, Y, Eugleninеae. X, *Euglena acus* (after Klebs); Y, *Phacus longicauda* (after Lemmermann). *a*, paramylon-grains (in X); *b*, longitudinal flagellum (in W); *c*, chromatophore; *f*, furrows (in V, W); *l*, leucosin; *m*, membrane of cyst (in N); *n*, nucleus; *o*, oil-drops; *p*, pyrenoid; *pl*, plug of cyst (in S); *s*, stigma; *t*, transverse flagellum (in W); *v*, contractile vacuole.

solid carbohydrates, in some cases starch, in others a compound akin to it. The motile cells (fig. 1 U) are pronouncedly dorsiventral, have two slightly unequal flagella (fig. 1 T), and possess a very specialised and characteristic structure. There is often a complex vacuolar system. The majority of the members are of flagellate organisation and sexuality (isogamous) is only reported in one form. The most advanced habit known is coccoid (p. 16). The class is relatively small and appears to be equally scantily represented in the sea and in freshwaters.

VI. *Dinophyceae* (*Peridinieae*), with usually numerous discoid chromatophores (fig. 1 W) which are dark yellow, brown, etc., and contain a number of special pigments. The products of photosynthesis are starch and oil (fat). The majority of the members are motile unicells and many possess a very elaborate cellulose envelope composed of a large number of often richly sculptured plates (fig. 1 V). Many species are colourless saprophytes or exhibit holozoic nutrition; one extensive series is parasitic. The motile cells are provided with two furrows, the one transverse (fig. 1 V, W, *f*) harbouring the transverse flagellum (*t*) which usually encircles the body, the other longitudinal and constituting the starting-point for the longitudinal flagellum which is directed backwards (fig. 1 W, *b*). Resting cysts of characteristic form are often produced (fig. 7 N). The most advanced habit is that of a branched filament. Isogamous sexual reproduction is certainly of rare occurrence and not yet clearly established. A class of mainly plankton organisms, more widely represented in the sea than in freshwaters.

VII. *Chloromonadineae*, with numerous discoid chromatopnores having a bright green tint and containing an excess of xanthophyll. Pyrenoids are lacking and oil is the assimilatory product. The few members of this class that are known are motile flagellates, with two almost equal flagella (cf. fig. 238). Although superficially like Xanthophyceae, the detailed structure of the cells is altogether different (complex vacuolar apparatus, etc.). The class is only recorded from freshwaters.

VIII. *Euglenineae*, with pure green chromatophores, each cell usually with several. Pyrenoid-like bodies are present in some forms; the product of photosynthesis is a polysaccharide, paramylon, which occurs in the form of solid grains of diverse and often very distinctive shape (fig. 1 X, *a*). Only flagellate members are known and the majority are motile with the help of one or two flagella which arise from the base of a canal-like invagination at the front end (fig. 1 X). There is a complex vacuolar system and a large and prominent nucleus. Only few cases of sexuality (isogamous) are known and these are not quite fully substantiated. The bulk of the members of this class probably inhabit freshwaters. The class is highly specialised and no really simple forms are known (cf. however p. 732).

IX. *Phaeophyceae*, with brown chromatophores containing, apart from the usual pigments, the yellow fucoxanthin. Naked pyrenoid-like bodies occur in some of the lower forms. The assimilatory products are alcohols (manitol) with only traces of sugars, as well as polysaccharides (laminarin) and fats, although most of the available data (67 *a*, 100) relate to the higher forms. Characteristic of the cell-contents of many forms are so-called fucosan-vesicles (fig. 2 C; *f*) which probably represent waste-products. The simplest types are filamentous (fig. 2 B), but the majority of the members are bulky parenchymatous forms, many attaining to a large size with complex external and internal differentiation (fig. 5 A, B). All but a few are marine (brown seaweeds). The motile reproductive cells (fig. 2 A) have two laterally attached flagella, of which one is directed forwards and the other backwards. These swarmers are always formed in special organs which are either unilocular (fig. 7 H) or septate with numerous small compartments (plurilocular sporangia, fig. 2 B, *p*). Sexual reproduction is of wide occurrence and ranges from isogamy to oogamy of a primitive type, with liberation of the ovum prior to fertilisation. The zygote exhibits no resting period. The life-cycle is very diverse, with varied types of alternation of generations.

X. *Rhodophyceae*, with red, blue (especially among freshwater forms), etc., chromatophores containing, apart from the usual pigments, others like the red phycoerythrin and the blue phycocyanin. Pyrenoid-like bodies are found in the lower groups and the product of assimilation is a solid polysaccharide similar to starch (Floridean starch, fig. 2 H, *a*). Neither motile reproductive stages nor flagellate members are known. The simplest forms are filamentous (fig. 2 I), but the majority attain to considerable complexity of structure (fig 2 K). Evident protoplasmic connections (fig. 2 D, K, *i*) are the rule between the cells of the majority of forms (except Bangiales). Most of the Rhodophyceae are marine (red seaweeds). All exhibit sexual reproduction of an advanced oogamous type, the female organ having a long receptive neck (fig. 2 D, E, *t*) and the antheridium producing but a single motionless male cell. As a result of fertilisation special spores (carpospores) are produced from bunches of threads that arise from the female organ (fig. 2 E, *g*) or in the higher groups from other cells with which the female organ becomes connected after fertilisation. The Rhodophyceae are either haploid or exhibit a regular alternation of similar haploid and diploid individuals, the latter bearing characteristic tetrasporangia, each producing four spores (fig. 2 I, *d*).

XI. *Myxophyceae* (*Cyanophyceae*), with a simple type of cell, containing at the best only a very rudimentary nucleus (central body) and without a proper chromatophore, the photosynthetic pigments being diffused through the peripheral cytoplasm (fig. 2 F). The pigments present are chlorophyll, carotin, phycocyanin, and phycoerythrin, the last two in varying proportions, the colour of the cells being very commonly blue-green. The products of photosynthesis are sugars and glycogen. No motile stages are known and all the members have a membrane around the cell. There is no sexual reproduction. The members of this class are of simple organisation and many propagate entirely by simple division or by vegetative means. The most advanced types are filamentous, many of them with a peculiar "false" branching

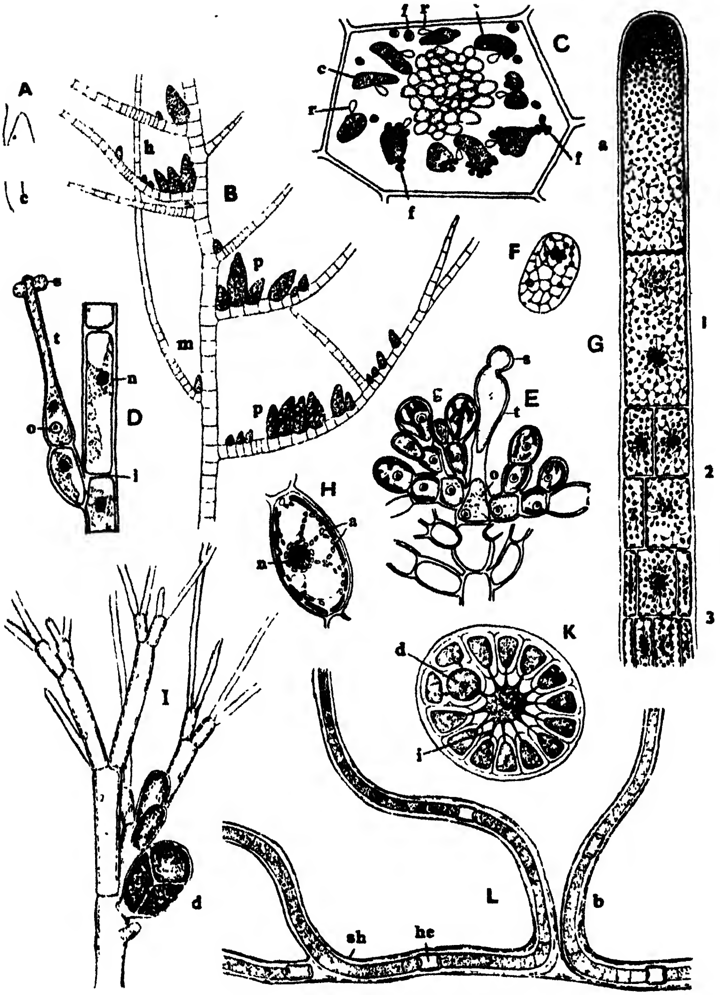

Fig. 2. Essential characteristics of the classes of the Algae. A–C, G, Phaeophyceae. A, zoospore of *Ectocarpus* (after Kuckuck); B, *E. coniferus*, showing trichothallic meristem (*m*), hairs (*h*), and plurilocular sporangia (*p*) (after Boergesen); C, cell of *Asperococcus*, showing fucosan-vesicles (*f*) and so-called pyrenoids (*r*) (after Kylin); G, apex of plant of *Sphacelaria*, showing the large apical cell (*a*) and its mode of segmentation (after Reinke). D, E, H–K, Rhodophyceae. D, female organ (carpogonium) of *Chantransia*, with female cell (*o*), trichogyne (*t*) and male cells (*s*) adhering to the tip of the latter (after

(fig. 2 L). They occur very abundantly in freshwaters and in terrestrial habitats, and are not uncommon in the sea.

It is not improbable that in the future the number of classes will have to be increased. There is still a considerable residue of colourless Flagellata that cannot be assigned to any one of the eleven preceding classes and whose exact relationship to other forms is unclear. They are therefore given a brief separate treatment at the end of this volume.

On the other hand there is some evidence for a closer relationship between some of the classes above distinguished. Thus, Pascher (132, 139, 147) has given considerable grounds for regarding Xanthophyceae, Chrysophyceae, and Bacillariophyceae as having originated from a common ancestry and has proposed to group them in the division Chrysophyta (cf. also (167)). In the same way there are indications of affinity between Cryptophyceae and Dinophyceae which Pascher classes in the division Pyrrophyta (132, 142, 147). These divisions would be of the same status as the Chlorophyta, Phaeophyta, Rhodophyta, Euglenophyta, and Myxophyta, each of which includes only a single class. These suggested relationships are fully discussed under the appropriate classes in the later portions of this book. At the present time it is perhaps best to regard each of the eleven classes as a separate evolutionary series until a clear relation to the others is indubitably established.

Our knowledge of the Algae is not confined to those existing at the present day, since a considerable number of fossil members are known (152). In the case of the larger calcified forms (cf. Dasycladaceae, Corallinaceae) the assignation of such fossils can be accomplished with a considerable degree of certainty, but in most other cases one is confronted with the difficulty that, in the absence of any data as to the nature of the cell-contents or of the methods of reproduction, reference to any particular class is well-nigh impossible. There can be no doubt that Algae have existed from the earliest geological epochs (123, 169), but the simpler unicellular, colonial, and filamentous types, quite apart from the difficulty of distinguishing them from mineral concretions, etc., only very rarely present any characteristics that admit of the determination of the class to which they belong. Many of those who

Kylin); E, fertilised carpogonium of *Batrachospermum*, showing the gonimoblasts (*g*) arising from the female cell (*o*) (after Kylin); H, cell of *Batrachospermum*, with Floridean starch (*a*) (after Schmitz); I, *Callithamnion corymbosum* with a tetrasporangium (*d*) (after Thuret); K, transverse section of a *Polysiphonia* showing protoplasmic connections (*i*) and a young tetrasporangium (*d*) (after Falkenberg). F, L, Myxophyceae. F, cell of *Merismopedia*, stained to show the structure (after Acton); L, thread of *Scytonema* showing false branching (*b*), heterocysts (*he*), and the sheath (*sh*) to the filaments (after Frémy). *e*, stigma; *c*, chromatophore; *n*, nucleus.

have dealt with such remains (cf. (13), (157)) are evidently unfamiliar with the marked parallelism that exists between the representatives of various algal classes (cf. p. 26).

THE RANGE OF STRUCTURE AMONG THE ALGAE

It is only in the Phaeophyceae and Rhodophyceae that the vegetative body attains to marked structural complexity, but many of the other classes show a progression from simple to more elaborate forms that is highly instructive as an object-lesson for the mode of origin of the multicellular plant. The following account of the range in structure to be met with among the Algae is not meant to afford more than an oversight that will facilitate comprehension of the general principles underlying the grouping of the members of the different classes and will prepare the way for their detailed consideration.

(*a*) The Motile Type

The motile unicell (figs. 1 C, J, K; 3 A, A′) which is represented in so many groups is commonly a more or less spherical, oblong or pear-shaped body, approximately circular in cross-section, although flattening (e.g. *Scourfieldia*, *Phacus*) as a mark of specialisation, often accompanied by the acquisition of a dorsiventral construction (Cryptophyceae, fig. 1 U), is found in many classes. The extremity directed forwards during movement and commonly bearing the flagella is spoken of as anterior, whilst the opposite one is posterior. The chromatophores occupy the posterior region or lie along the sides, while the nucleus is frequently situated near the middle of the cell. When a cell-wall is present the surface-layer of the protoplast is constituted by a plasma-membrane, but in the numerous naked forms it is developed as a more or less rigid *periplast* that either admits of extensive change of shape (so-called *metaboly*, well seen in many species of *Euglena*) or gives the unicell a firm contour (*Cryptomonas*, fig. 1 U; *Phacus*, fig. 1 Y). It is distinguished from a cell-wall by the fact that it normally divides with the protoplast.

Many of the naked flagellate forms at times withdraw or shed their flagella and exhibit a creeping amoeboid movement with the protrusion of blunt pseudopodia,[1] which conditions a constant change of shape and is only possible where the periplast is soft or after the latter has been discarded (Chrysophyceae, p. 532).[2] In other cases the organism in these non-flagellate phases develops long delicate cytoplasmic

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[1] With reference to the mechanism of these movements, see (51), (130).

[2] Such amoeboid movement is also seen at times in the reproductive cells of various Green Algae (131) and Bangiales. Chadefaud (18) has recorded a similar protrusion of pseudopodia on the part of the cytoplasm in algal cells invested by a definite membrane.

processes known as *rhizopodia* (fig. 3 N), whose length and number are continually altering (cf. also *Heterochloris*, fig. 154 D and *Chrysamoeba*, fig. 176 B). Such stages lead over to permanently amoeboid or rhizopodial forms, met with in various classes and very strongly represented among Chrysophyceae (p. 534).

In several classes there occur, side by side with the ordinary motile unicells, other types in which the cell is surrounded by a special, usually rigid and variously shaped envelope, provided with apertures for the protrusion of the flagella and separated from the cell proper by a space (*Phacotus*, fig. 3 C; *Chrysococcus*, fig. 3 C′). Such types are spoken of as *encapsuled*. They occur both among forms in which the individual is naked and among those in which it is provided with a cell-wall, and a considerable number of such organisms have adopted an epiphytic habit (especially among Chrysophyceae, p. 523). These sedentary forms either retain their flagella or lose them, their place being sometimes taken by simple or branched thread-like rhizopodia (fig. 171 D).

Another special development of the motile unicell is seen in the *colourless forms* which are met with in various classes and which, except for the absence of chromatophores, so closely resemble the pigmented forms that an undoubted affinity exists (*Polytoma*, fig. 3 D; *Monas*, fig. 3 D′). Such colourless forms are either saprophytic or holozoic. Pascher (135) has, among Chlorophyceae and Chrysophyceae (pp. 90, 538), described forms with much reduced chromatophores which clearly point the way in which such colourless types have originated. They are probably an outcome of the saprophytic tendencies exhibited by many motile unicellular organisms. A number of the colourless forms in various classes (Xanthophyceae, Chrysophyceae, Dinophyceae) are normally amoeboid or rhizopodial (137), but these may have originated direct from pigmented types with the same habit. It is probably legitimate to conclude, as Pascher (136, 137) does, that all such amoeboid and rhizopodial types are secondarily derived from flagellate forms (cf. however (40)). When they are colourless it may be impossible to recognise their true affinities unless some characteristic trait of the ancestor be retained.

Further evolution of the free-moving individual has taken place in the direction of the *motile colony* (fig. 3 B, B′). Here varying numbers of unicells are aggregated together in different ways, often within a mucous envelope, to form usually spherical groupings in which all the individuals are alike and complete in themselves, although they do not normally occur separately; all contribute by the joint action of their flagella to the movement of the colony. Whilst in the majority of cases there is no appreciable differentiation among the individuals, a few Chlorophyceae have colonies in which certain larger cells are set aside to fulfil the reproductive functions, the others being purely

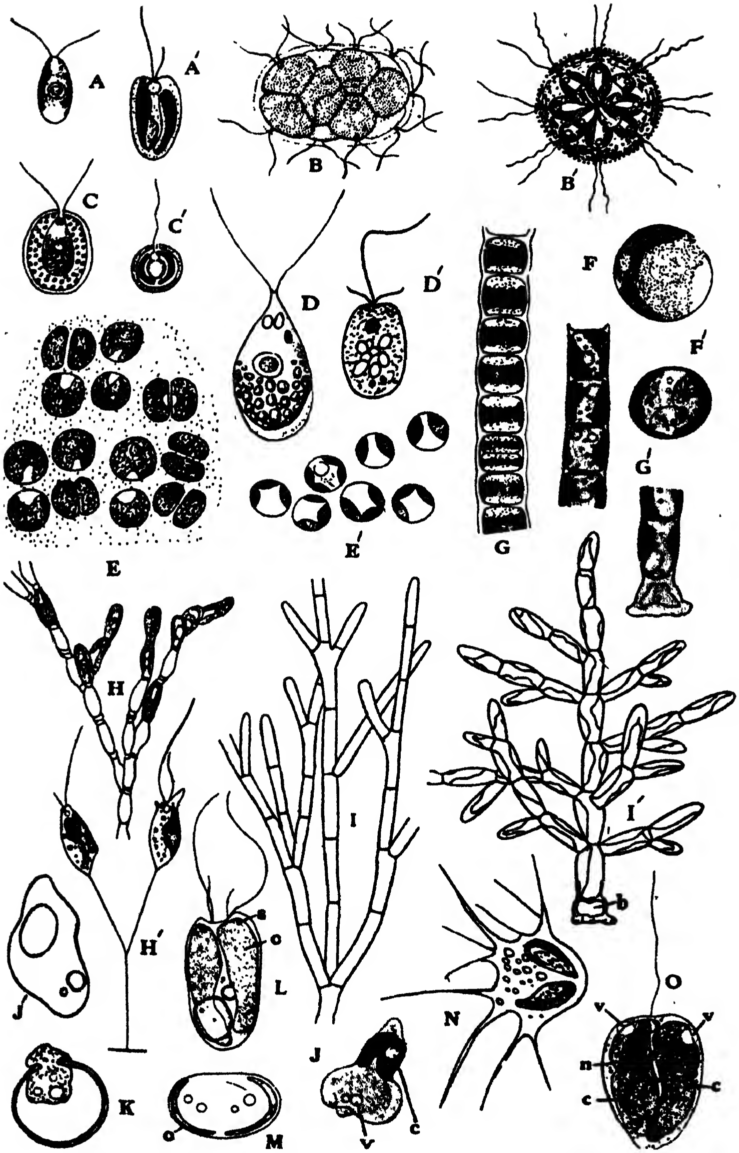

Fig. 3 [*for description see opposite*]

vegetative (*Pleodorina*, *Volvox*, p. 106). Such colonial forms are scarcely to be distinguished from multicellular individuals.

One of the most remarkable developments of the free-moving unicell are the *double individuals*, long known among the Distomatineae (Diplozoa) ((75) p. 116, (87)), a group of colourless Flagellata (p. 753), while a number of similar types have recently come to light among the Chrysophyceae. In these cases the individual betrays its double nature by the possession of one or more of the essential cell-organs in duplicate. In Korschikoff's *Amphichrysis* ((96) p. 261) (fig. 3 O) it is the chromatophores and contractile vacuoles, in Pascher's *Didymochrysis* (143) (fig. 3 L, M) also the flagella and eye-spots that are paired, while in the Distomatineae even the nuclei are in duplicate (cf. fig. 245 F, p. 751). *Amphichrysis* is a double *Chromulina*, *Didymochrysis* a double *Ochromonas*. Pascher (143) believes that such forms have arisen as a result of a division-process arrested at various steps, the incompletely halved individual then continuing to propagate as though it were a single unit. Cases of such incomplete division are not unknown in members of various algal groups, and Chatton (19), by preventing the completion of division in *Glaucoma* (Infusoria), was able to obtain such double individuals which propagated by division. Pascher rightly draws attention to the further parallel constituted by the compound zoospore of *Vaucheria* (p. 431).

(*b*) Palmelloid and Dendroid Types

In a very large number of cases, especially among the forms showing "algal" organisation, motility has disappeared during the vegetative phase and is resorted to solely at times of reproduction. The beginnings of this tendency are plainly discernible among the free-moving unicellular types. Thus, in species of *Chlamydomonas* (Chlorophyceae)

Fig. 3. A–I, Parallel forms in Chlorophyceae and Chrysophyceae. A, *Chlamydomonas* (after West) and A′, *Ochromonas* (after Pascher), motile unicell. B, *Pandorina* (after Smith) and B′, *Syncrypta* (after Stein), motile colony. C, *Phacotus* (after West) and C′, *Chrysococcus* (after Klebs), encapsuled type. D, *Polytoma* (after Francé) and D′, *Monas* (after Lemmermann), motile colourless type. E, *Tetraspora* (after Reinke) and E′, *Phaeocystis* (after Lagerheim), palmelloid type. F, *Chlorococcum* (after Pascher) and F′, *Chrysosphaera* (after Pascher), coccoid type. G, *Ulothrix* (after Klebs) and G′, *Nematochrysis* (after Pascher), simple filament. H, *Prasinocladus* (after Davis) and H′, *Chrysodendron* (after Pascher), dendroid colony. I, *Cladophora* (after Migula) and I′, *Phaeothamnion* (after Pascher), branched filament. J, amoeboid swarmer of *Aphanochaete* (after Pascher) and J′, K, *Leucochrysis* (after Pascher); J′, amoeba; K, escape of amoeba from cyst. L, M, *Didymochrysis paradoxa* (after Pascher); M, optical transverse section. N, *Synura*, rhizopodial stage (after Pascher). O, *Amphichrysis compressa* (after Korschikoff). *b*, basal cell (in I′); *c*, chromatophore; *n*, nucleus; *s*, stigma; *v*, contractile vacuole.

and *Chromulina* (Chrysophyceae) the individuals at times lose their flagella and undergo successive division with a simultaneous development of mucilage-envelopes, so that there result big gelatinous masses comprising numerous cell-generations and sometimes attaining sufficient dimensions to be plainly visible to the naked eye. These "*Palmella*"*-stages* are, in the case of the organisms just mentioned, usually temporary phases in the life-cycle, since sooner or later the contained cells acquire flagella and again adopt the swarming habit. The conditions calling forth the development of these palmelloid stages in nature are hardly known, but, apart from the suppression of motility, factors causing gelatinisation of the membranes must be involved (cf. (191)).

A large number of genera are known in which this *palmelloid habit* is the permanent one (e.g. *Tetraspora* among Chlorophyceae, fig. 3 E · *Chlorosaccus* among Xanthophyceae; *Phaeocystis* among Chrysophyceae, fig. 3 E′), the reproductive cells alone being motile. All such forms are colonial, the component cells, except for their aggregation within a common mucilage-envelope, being quite independent of one another and fulfilling all the functions of an individual. The colonies are often of quite irregular and indefinite shape, like the *Palmella*-stages above mentioned. The mucilage is either secreted by the protoplasts of the cells or arises by the gelatinisation of their membranes (85, 165, 190). Alone among Chrysophyceae have such colonies attained a higher differentiation (p. 546).

A variant of the type just considered in which the mucilage is produced locally, generally at the base of the cell, results in *dendroid colonies*, such as those of *Prasinocladus* among Chlorophyceae (fig. 3 H) and *Chrysodendron* among Chrysophyceae (fig. 3 H′). The polarity thus expressed probably marks a fundamental difference from the ordinary palmelloid habit, and the practice of classing the two series of forms in the same family is to be deprecated. In *Dinobryon* (Chrysophyceae) somewhat similar dendroid colonies are motile. Both the palmelloid and dendroid habits are to be regarded as closely allied to the free-swimming one, since in either case a reversion to the motile condition very readily occurs.

(*c*) THE COCCOID HABIT

In many of the motile unicellular types the individual comes to rest and draws in its flagella before division of the protoplast to form a new generation of free-moving unicells takes place. A prolongation of this sedentary phase, with an accompanying restriction of the swarming period, would lead ultimately to a motionless unicellular individual resorting to motility only at times of reproduction. This *coccoid habit* is the permanent one in a very large number of Chlorophyceae (e.g. *Chlorococcum*, fig. 3 F) and is also encountered in many other classes (*Chrysosphaera* among Chrysophyceae, fig. 3 F′, etc.). A further step in the same direction leads to the complete disappearance of motility (138), the reproductive cells being motionless from the first and resembling the parent in all but size (azoosporic forms, e.g. *Chlorella*, fig. 37 C, I). The cells of the coccoid type are commonly spherical, but other shapes are also realised. Among these sedentary forms there often exists a very strong colonial tendency,[1] nowhere more highly developed than in the Chlorophyceae, where almost every conceivable type of motionless colony is to be found (p. 159).

Many of the sedentary forms so far noticed betray their close relation to the motile types by the possession of contractile vacuoles and eye-spots (97, 148).

(*d*) THE ORIGIN AND CHARACTERISTICS OF THE FILAMENTOUS HABIT

It is distinctive of all the types of algal habit so far discussed that, when cell-division occurs, the products of division of the protoplast, unless they remain permanently naked, sooner or later become completely invested by new cell-walls of their own. The membrane of the parent-cell is either ultimately cast off or, in some of the colonial forms, becomes mucilaginous. Cell-division in these cases therefore leads to the formation of new units which are quite independent of the membrane of the parent-cell, and is thus really solely concerned with reproduction. Moreover, successive divisions usually take place in planes at right angles to one another. The more highly evolved forms to be considered below are, however, characterised by a type of cell-division (*vegetative division*) in which the parent-cell ordinarily divides without rupture or gelatinisation of its wall, the two units produced by division of the protoplast being merely separated by the development between them of a strip of membrane which is joined laterally to the membrane of the parent. Among unicellular forms this type is seen only in a number of Green Algae (Chlorosphaeraceae, Pleurococcaceae), most of which are probably reduced filamentous types. Vegetative division affords the starting-point for the cellular plant.

Pascher has drawn attention to the fact that cell-division in cellular Algae in so far differs from that of higher plants in that the dividing septum usually shows no relation to the nuclear spindle, no cell-plate being formed (cf. however p. 71). He further (140, 145) asserts that the customary interpretation of cell-division in filamentous types as given

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[1] With reference to the conditions inducing the development of colonies in these forms, see (61), (191).

above is erroneous, inasmuch as septa connected with the walls of the mother-cell are not formed. According to him, after the protoplast has divided into two, each half-protoplast becomes enveloped in a completely new wall, the apparent septum being constituted by the double layer of membrane formed by the adjacent walls of the daughter-cells. In other words the cell-division of a filamentous alga is regarded as being of just the same type as in the unicellular forms above considered, except that there is no marked contraction of the protoplast so that the daughter-cells completely fill out the parent-membrane and that the latter persists around the daughter-individuals. While this interpretation appears to apply to a number of simple filamentous types (some Chrysophyceae; *Dinothrix*, fig. 237 A), it is difficult to harmonise it with the many accounts existing in the literature (cf. e.g. (173)) of the gradual ingrowth of a dividing septum during cell-division in green filamentous Algae (figs. 69 D, E, I; 99 A). The data at present published by Pascher, as well as those afforded by Vischer (192), do not include a detailed consideration of such cases and one must await a fuller account before estimating their true value (cf. also (155) p. 6). Each cell of a filament of course develops its own appropriate thickening-layers subsequent to cell-division, and in later stages the primary septum is often indistinguishable. The question to be settled is whether there is such a primary septum or not, and that can only be determined by a careful study of cell-division.

According to Pascher ((140); cf. also (68)) the division of the protoplast in many filamentous forms takes place in the longitudinal plane, although rotation to the transverse plane ensues after its completion so that the cells lie one in front of the other (cf. fig. 183 F, G). In other cases there is more or less marked rotation of the protoplast to the transverse plane before division, so that the direction of the latter comes to be oblique or even transverse.

Division of the vegetative type constitutes the characteristic of the *filamentous habit* which in fact owes its origin to the adoption of this method of segmentation and to its taking place time after time along the same plane transverse to the long axis of the filament. There can be little doubt as to the mode of origin of filamentous Algae, since in many of the simpler forms it is recapitulated every time a motile swarmer comes to rest on some substratum and, after secreting a cell-wall, proceeds to divide by vegetative division to form the thread. The latter was no doubt in most cases a direct further development from the motile unicell after the latter had adopted an epiphytic habit.[1] The filament is the most elementary type of *thallus*, as the multicellular body of the Algae is conveniently called. In its simplest form it is seen in such genera as *Ulothrix* (fig. 3 G), *Tribonema*,

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[1] Epiphytic unicells are abundantly represented in many classes (cf. e.g. p. 151). There is no evidence for the view that derives the filament from palmelloid types.

Nematochrysis (fig. 3 G′), and many Myxophyceae, where it consists merely of a row of cells firmly connected with one another.

Two modifications of this type of plant-body are frequent. If septa arise along two planes at right angles to one another we obtain flattened leaf-like expanses, such as occur in *Ulva* (Chlorophyceae, fig. 62 E), *Punctaria* (Phaeophyceae), and *Porphyra* (Rhodophyceae); foliaceous thalli of this kind may consist of two or more layers of cells owing to the occurrence of a few divisions in the plane parallel to the surface of expansion. Such *parenchymatous forms* may at times assume other shapes, for example a tubular one, well seen in *Enteromorpha* (Ulvaceae, fig. 63 B) and *Asperococcus* (Phaeophyceae) and resulting from a subsequent separation of the layers composing the thallus. The parenchymatous habit is of special interest, since it shows how from a filamentous beginning a flat expanse may originate.

More frequent is the development of a branching filament owing to the lateral outgrowth of more or less numerous cells, the outgrowths undergoing transverse septation like the main thread. Such branched filaments are to be found in all classes in which the filamentous habit has appeared and represent in many cases the highest type of development that has been reached. Examples are afforded by *Cladophora* (Chlorophyceae, fig. 3 I), *Phaeothamnion* (Chrysophyceae, fig. 3 I′), *Callithamnion* (Rhodophyceae, fig. 2 I), etc. A peculiar form of false branching is distinctive of many Myxophyceae (fig. 2 L).

In many of the simpler unbranched filamentous forms (*Ulothrix*, *Spirogyra*) all the cells are quite alike and every one is capable of growth and division, as well as of the formation of reproductive units. Such growth may well be described as *diffuse*.[1] Forms like these are but little removed from colonies, except in the close association of their cells and in the fact that there is probably always some give and take at times of reproduction, since all the cells are rarely involved in the formation of spores or gametes, though potentially every one is capable of it. Moreover, in most cases filamentous forms tend at least at first to be attached by a specially modified basal cell (11, 153, 177), which in the mature condition generally has a very scanty protoplast and is usually incapable of forming reproductive elements; these cells are often very firmly cemented to the substratum. Similar *haptera* are encountered in the branched filamentous types (e.g. *Bulbochaete*; *Phaeothamnion*, fig. 3 I′, *b*), but here there is often further-going division of labour.

Thus, in a few members of the Green Algae (*Cladophora*) growth and division are mainly restricted to the end-cells of the branches and such apical cells are even more sharply circumscribed among the Charales (p. 448), the Sphacelariales (Phaeophyceae, fig. 2 G, *a*), and

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[1] The term *intercalary* is often used, but that is best confined to cases where there is a well-defined meristem not located at the apex.

the Red Algae (cf. below). A definite growing point of another type is not uncommon among the filamentous Ectocarpales (Phaeophyceae). Here, where the branches of the filaments terminate in colourless hairs (fig. 2 B, *h*), cell-division is often confined to an intercalary meristem (*m*) of a few cells situated at the base of the hair. Such *trichothallic growth* is also encountered among the Rivulariaceae (Myxophyceae), whilst in the Cutleriales (Phaeophyceae) the body is built up of large numbers of threads with trichothallic growth which undergo congenital fusion just beneath the meristem.

In the more advanced filamentous Algae formation of reproductive cells is often practically confined to the ultimate branches, the principal (and sturdier) ones serving in the main only a supporting function. In *Draparnaldia* and *Draparnaldiopsis* (cf. the frontispiece) among Chlorophyceae and *Batrachospermum* among Rhodophyceae, for instance, the cells of the main axes are much larger and differ somewhat in form from those of the laterals, while in *Draparnaldia* they have only a scanty chloroplast. In such cases therefore there is pronounced division of labour between the different parts of the filament.

(*e*) The Heterotrichous Habit

The most highly evolved type of filamentous plant-body is the *heterotrichous* one ((49) p. 111) which is characteristic of the Chaetophorales among Chlorophyceae, where it represents the highest differentiation reached, and of many of the simpler Phaeophyceae and Rhodophyceae; it also occurs among the Chamaesiphonales (Myxophyceae) and in a simple form in *Dinoclonium* (Dinophyceae). In all such cases the thallus consists of two distinct parts (fig. 4 A, C), viz. (i) a prostrate creeping system (*c*), usually performing *inter alia* the functions of a holdfast and exhibiting apical growth, and giving rise to (ii) a projecting or erect system (*e*) composed of one or more, usually branched, filaments which trail out into the water. All possible stages in the relative development of the two systems are met with in the representatives of the different classes where this type of habit is found.

By a compacting of the filaments of the prostrate base into a one-layered stratum and a more or less complete disappearance of the erect system, flat attached *discoid forms* have originated, such as are excellently illustrated by the common species of *Coleochaete* (fig. 87 A) among Chlorophyceae, by *Ascocyclus* among Phaeophyceae, and by *Erythrocladia* (fig. 4 B) among Rhodophyceae (Bangiales). In such discs the filamentous construction is either still plainly recognisable (nematoparenchymatous forms, fig. 4 B) or it may be completely obscured (blastoparenchymatous forms).[1]

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[1] Terms used by Geitler in describing the Chamaesiphonales.

Similar types, with a compacted prostrate system in which every cell bears an upright filament, simple or branched and more or less closely juxtaposed and often concrescent, appear as *crusts* or *cushions*. Such are exemplified by *Pseudopringsheimia* (Chaetophorales, fig. 77 B), *Ralfsia* (Phaeophyceae, fig. 4 F), *Hildenbrandia* (Rhodophyceae, fig. 4 G), *Oncobyrsa* (Myxophyceae), etc. A large proportion of the characteristic multicellular epiphytes belong to these discoid or crust-forming types.

In nearly all the heterotrichous groups, however, another tendency is evident, viz. the practical elimination of the prostrate and the elaboration of the erect system. This gives us *Draparnaldia* and *Draparnaldiopsis* (frontispiece) among the Chaetophorales, forms like the Sphacelariales among Phaeophyceae, and such types as *Batrachospermum* among Rhodophyceae. In fact it is probably not going too far to say that the heterotrichous habit underlies the whole construction of many, if not of all, of the more advanced brown and red seaweeds, a point of view that will be fully elucidated in the consideration of these forms in the second volume. The potentialities of this habit, with the possibility for the evolution of both prostrate and erect types, are perhaps not without their significance in connection with the origin of the two alternating generations in some of the higher plants ((48, (49) p. 145).

(*f*) The Siphoneous Habit

In a number of the Algae considerable enlargement of the plant-body may take place without any septation occurring. Thus a large multinucleate structure originates (e.g. the common *Vaucheria*), generally called a *coenocyte*, though sometimes rather erroneously spoken of as unicellular, since such forms are best interpreted as multicellular plants lacking the usual septation. This *siphoneous habit* is most markedly developed among Siphonales (Chlorophyceae), but is also seen in *Botrydium* (Xanthophyceae, fig. 164). In the absence of the usual support afforded by the septa, other methods for securing mechanical efficiency have been adopted and these largely run parallel with similar devices found among the septate forms of other classes, affording indeed the only examples of these types of construction among the Green Algae.

(*g*) The Advanced Types of Algal Construction

The further evolution of the filamentous plant-body, whether septate or not, has followed three chief lines, viz. (i) the close juxtaposition of the branch-systems of a single main axial thread to form more or less compact pseudoparenchymatous thalli (*uniaxial construction*.

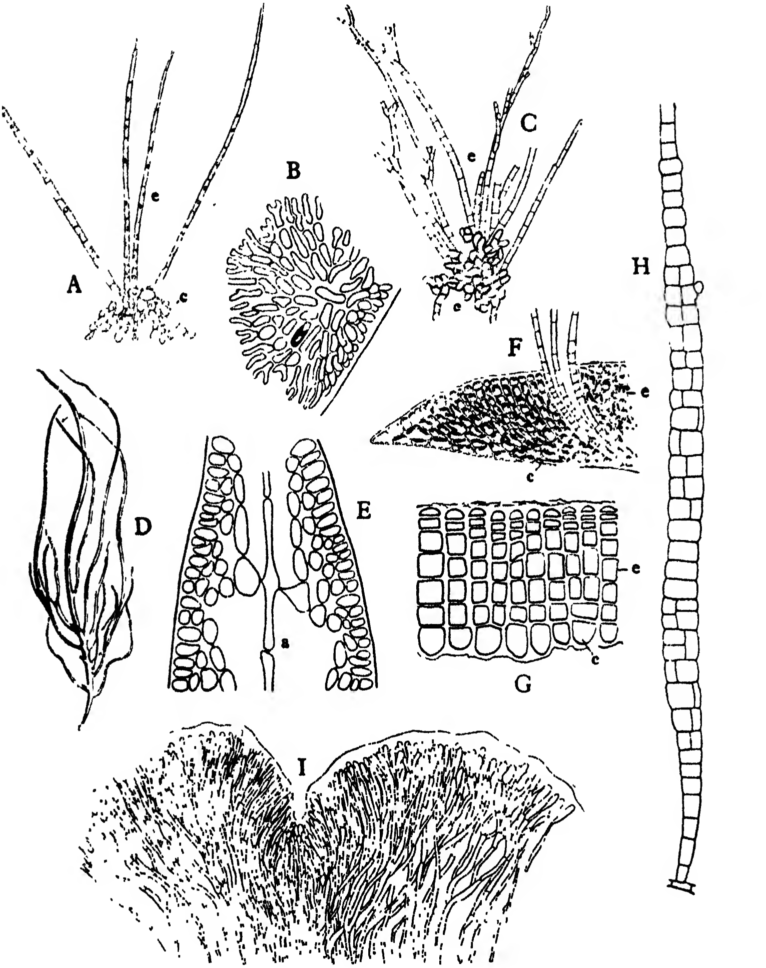

Fig. 4. The advanced types of algal habit. A, *Stigeoclonium*, heterotrichous filament (after Fritsch). B, *Erythrocladia* (Bangiales), discoid type (after Rosenvinge). C, *Chantransia*, heterotrichous filament (after Rosenvinge). D, E, *Dumontia incrassata* (Rhodophyceae); D, habit (after Kützing); E, longitudinal section of thallus (after Kylin). F, *Ralfsia* (Phaeophyceae), crust in section (after Reinke). G, *Hildenbrandia* (Rhodophyceae), crust in section (after Fritsch). H, *Litosiphon pusillus* (Phaeophyceae) (after Sauvageau). I, *Scinaia furcellata*, apex in longitudinal section (after Svedelius). *c*, creeping, and *e*, erect systems; *a* (in E), axial thread.

fig. 4 E), (ii) the close juxtaposition of a number of threads so that the central axis consists of a strand of filaments whose numerous branches form a more or less compact cortex (*multiaxial construction*, figs. 4 I; 133 A, E), and (iii) the division of the cells of the primary filament by septa in all directions to form a parenchymatous body (*parenchymatous forms*, fig. 4 H). The first two types of construction form the fundamental basis of the structure of all Florideae (Rhodophyceae) where indeed the thallus, no matter what its outward form, is always derivable from a filament or filaments with pronounced apical growth, although the simple branched thread is comparatively rare. The uniaxial construction is seen in a simple form in *Batrachospermum* where the filamentous nature is still clearly recognisable. A more compact form is, however, attained in Red Algae like *Dumontia* (fig. 4 D), where the origin from a branched thread is recognisable only in sections (fig. 4 E), while in many of the advanced types like the Delesseriaceae it is only by careful study and by observing the arrangement of the protoplasmic connections between the cells (cf., p. 9) that the origin of the foliaceous thallus from such a uniaxial branch-system can be deciphered. Similarly, a multiaxial construction, while clearly evident in such an alga as *Nemalion* or *Scinaia* (fig. 4 I), appears in *Furcellaria* in a more compacted form, whilst in *Chondrus* the leafy thallus betrays its actual structure only after laborious investigation.

The same two types of construction are found in other classes. Thus, among Siphonales the uniaxial type obtains in Dasycladaceae (p. 387), here combined with calcification to form an often rigid plant-body, whilst the multiaxial type is essentially characteristic of the Codiaceae (p. 402). In Phaeophyceae the latter type is widely represented among the Ectocarpales (*Castagnea*, *Leathesia*, etc.). In the red and brown seaweeds these elaborate forms not uncommonly arise from a primary heterotrichous filament, the kind of ultimate structure realised depending on whether one or a number of threads of the erect system are concerned in the production of the mature thallus.

The third method, the derivation of a parenchymatous body from a primary filament by abundant septation is, apart from the origin of foliaceous expanses in some Green and Red Algae already referred to above (p. 19), met with only in the Phaeophyceae. In a simple form it is seen in a large number of Ectocarpales (haplostichous forms, e.g. *Scytosiphon* or *Litosiphon* (fig. 4 H) and Sphacelariales (fig. 2 G)), but it has also led to the evolution of the large parenchymatous body met with in the big brown kelps belonging to the Laminariales (fig. 5 A) and Fucales. Such a parenchymatous construction occurs both in forms with diffuse growth (Ulvaceae, *Porphyra*), as well as in those with a circumscribed growing-point, either intercalary (Laminariales) or apical (Sphacelariales, fig. 2 G, Dictyotales, Fucales).

In the large brown seaweeds the thalli exhibit marked anatomical differentiation (cf. fig. 5 B, F), even extending to the development of true sieve-tubes in *Macrocystis* and *Nereocystis*, but as compared with the internal differentiation met with in higher plants there are two prominent points of divergence. In the first place the tissues are not sharply contrasted, since one can gradually merge into and even give rise to another at its inner limit. In the second place there is an abundant production of unbranched or branched filamentous outgrowths (so-called *hyphae*, fig. 5 F, *h*) from many of the internal cells, these threads worming their way—often in very large numbers—through the soft mucilaginous membranes of the cells forming the central part of the thallus. These hyphae probably largely serve a mechanical purpose, and in their widespread occurrence, as well as in the above-mentioned intergrading of tissues, we have marked points of contrast in the structure of these elaborate forms as compared with higher plants.

The production of thread-like outgrowths from the cells of the multicellular thallus is altogether a very frequent method for increasing rigidity in brown and red seaweeds, although in Chlorophyceae it is met with only in *Draparnaldia*, *Draparnaldiopsis* (frontispiece), and in *Chara* (fig. 148). In many cases the threads grow superficially over the older parts of the primary thallus (so-called *cortical threads*) and may very considerably increase their thickness, as in *Desmarestia* (fig. 5 C), *Sphacelaria*, *Polysiphonia*, etc. It is probable that both hyphae and cortical threads are morphologically of the same nature as the attaching rhizoids found in many filamentous Algae. They do indeed play a considerable rôle in forming the sucker-like attaching discs of Fucales and the branched haptera of Laminariales (fig. 5 A, *a*).

(*h*) Epiphytes, Endophytes, Parasites

Very common among the Algae is the *epiphytic habit* (i.e. growth on some other living plant, often a larger alga).[1] This is met with in more or less numerous representatives of all classes and has already repeatedly been referred to. It is probably no far step from epiphytism to endophytism, and in many genera that are normally epiphytic endophytic forms are not uncommon. Thus, in species of *Stigeoclonium*, *Ectocarpus*, and *Chantransia*, the prostrate system may be endophytic in the superficial tissues of other larger Algae and, when the upright system is reduced, the whole thallus may become endo-

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[1] A large proportion of the Algae and especially of the seaweeds are, however, lithophytes, i.e. they grow on rocks or stones.

phytic, as in *Endoderma* (Chaetophorales, fig. 5 G), *Streblonema* (Ectocarpales, fig. 5 D), etc. In how far such forms are mere space-parasites (as in the case of *Chlorochytrium*, fig. 5 E) or derive some nourishment from the host is scarcely definitely settled in any one case. The fact that individual species are commonly confined to one particular host or even one definite part of the host points to some kind of interrelation; on the other hand, there is in most cases little

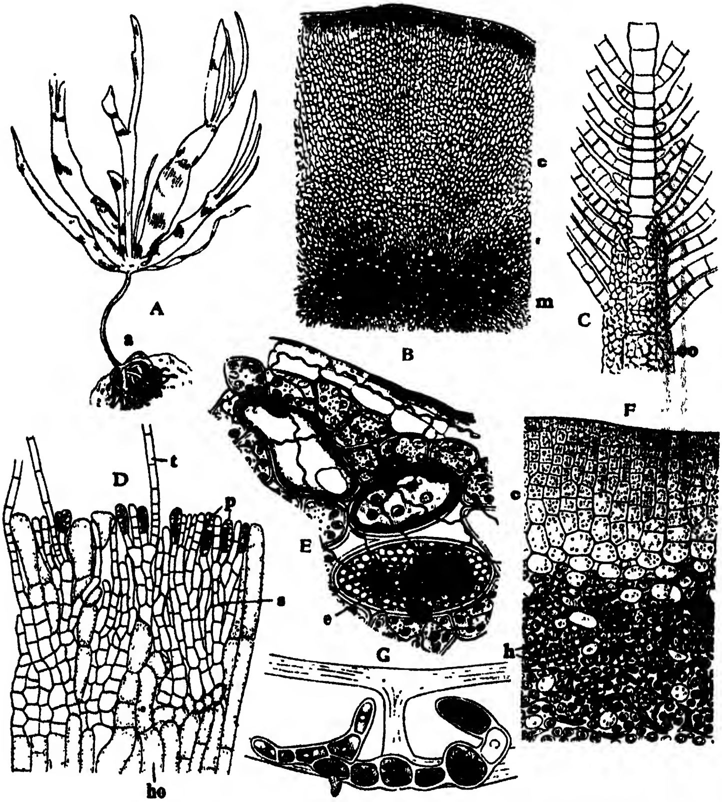

Fig. 5. The advanced types of thallus construction. A, *Laminaria*, habit (after Fritsch and Salisbury). B, *Laminaria*, section of the stipe (after Oltmanns). C, *Desmarestia*, apex of a growing plant (after Reinke). D, *Streblonema* (*s*) endophytic in *Fucus* (*ho*) (after Kylin). E, *Chlorochytrium*, resting cells (*e*) endophytic in *Lemna* (after Klebs). F, *Fucus*, section of midrib (after Oltmanns). G, *Endoderma*, endophytic in the membrane of *Ectocarpus* (after Wille). *a*, attaching organ; *c*, cortex, *co*, cortical threads; *h*, hyphae; *m*, medulla; *p*, plurilocular sporangia; *t*, hair.

TABLE SHOWING PARALLELISM IN EVOLUTION OF THE SIMPLER TYPES OF ALGAL CONSTRUCTION IN FIVE CLASSES OF PROTOPHYTA

TYPE OF CONSTRUCTION	CHLOROPHYCEAE	XANTHOPHYCEAE	CHRYSOPHYCEAE	CRYPTOPHYCEAE	DINOPHYCEAE
(*a*) Motile holophytic unicell[1]	Chlamydomonas, etc.	Heterochloris, etc.	Chromulina, etc.	Cryptomonas, etc.	Gymnodinium, etc.
(*b*) Motile colourless unicell[1]	Polytoma, etc.	Chloramoeba (facultative)	Monas, etc.	Chilomonas	Bernardinium, etc
(*c*) Encapsuled unicell[2]	Phacotus, etc.		Chrysococcus, etc.		
(*d*) Motile colony	Pandorina, etc.		Synura, etc.		Polykrikos
(*e*) Dendroid colony[3]	Prasinocladus, etc.	Mischococcus	Chrysodendron		—
(*f*) Palmelloid colony[4]	Tetraspora, etc.	Chlorosaccus, etc.	Chrysocapsa, etc.	Phaeococcus	Gloeodinium
(*g*) Coccoid (zoosporic)	Chlorococcum, etc.	Botrydiopsis, etc.	Chrysosphaera	Tetragonidium	Cystodinium, etc.
(*h*) Coccoid (azoosporic)	Chlorella	Chlorobotrys, etc.	—		Hypnodinium
(*i*) Simple filament[4]	Ulothrix, etc.	Tribonema, etc.	Nematochrysis		Dinothrix
(*j*) Heterotrichous filament[5]	Stigeoclonium, etc.		Cf. Phaeodermatium		Dinoclonium
(*k*) Siphoneous type	Vaucheria, etc.	Botrydium	—		
(*l*) Holophytic amoeboid type		Rhizochloris	Chrysamoeba		Gymnodinium (p. 704)
(*m*) Holozoic amoeboid type[6]	Gametamoeba		Leukochrysis		Dinamoebidium
(*n*) Plasmodial type	Chlamydomonas sp. (p. 111)	Chlorachnion, etc.	Myxochrysis		Cf. Paradinium (p. 688)

Also in Chloromonadineae and Euglenineae.

Cf. *Trachelomonas*, etc., among Euglenineae.

Cf. *Colacium* among Euglenineae and *Gomphonema*, etc., among Bacillariophyceae.

Also in Myxophyceae.

Also in Phaeophyceae, Rhodophyceae, Myxophyceae.

Cf. p. 732 among Euglenineae.

evidence of any damage to the tissues except in the immediate neighbourhood of the endophyte. Undoubted algal parasites are, however, known. Striking examples, where the parasitism is accompanied by loss of photosynthetic pigments, are afforded by *Rhodochytrium* (p. 157) and *Phyllosiphon* (p. 426) among Chlorophyceae and *Harveyella* and *Choreocolax* among Rhodophyceae. Algae of several classes enter into symbiosis with Fungi or diverse animals (cf. especially pp. 186, 658).

(*i*) PARALLELISM

In reviewing the main types of habit found in the different classes of Algae one of the most striking facts that emerges is the abundant parallelism (cf. figs. 3 and 4 and the tables on pp. 26, 27). The motile unicell, the encapsuled type, the motile colony, the palmelloid, coccoid, and filamentous types, the heterotrichous filament, as well as the more specialised forms of thallus with a uniaxial or multiaxial structure, not only occur again and again, but quite analogous modifications of them are often to be recognised in different classes. In many cases indeed it is only by a careful study of the cell-structure or reproductive organs that quite unrelated forms can be distinguished, the outward habit being practically identical (cf. e.g. (149)). The history of algal taxonomy is full of examples of the non-recognition of this fact having led to the grouping together of species that

TABLE SHOWING PARALLELISM IN EVOLUTION OF ADVANCED TYPES OF ALGAL CONSTRUCTION

TYPE OF CONSTRUCTION	CHLOROPHYCEAE	PHAEOPHYCEAE	RHODOPHYCEAE
(*a*) Heterotrichous filament	Stigeoclonium, etc.	Ectocarpus, etc.	Chantransia, etc.
(*b*) Discoid (prostrate) type[1]	Protoderma, etc.	Ascocyclus, etc.	Erythrocladia
(*c*) Crusts or cushions (cf. p. 21)[1]	Pseudopringsheimia	Ralfsia, etc.	Hildenbrandia, etc.
(*d*) Elaborated erect type	Draparnaldia Draparnaldiopsis	Desmarestia	Batrachospermum
(*e*) Compact (pseudoparenchymatous) type (uniaxial)	Dasycladaceae (siphoneous)		Lemanea, etc.
(*f*) The same (multiaxial)	Codiaceae (siphoneous)	Castagnea, etc.	Nemalion, etc.
(*g*) Foliose, parenchymatous type	Ulvaceae	Punctaria	Porphyra
(*h*) Tubular parenchymatous type	Enteromorpha	Asperococcus	

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[1] Also in *Pleurocapsa*, *Oncobyrsa*, etc. (Myxophyceae)

belonged to quite different classes. Moreover, since outward form is in many cases of little or no value in determining the affinity of an alga, it is quite impossible to establish with any measure of certainty the systematic position of the simpler types of Algae found in the fossil condition.

With the evidence of this marked parallelism before one, it can hardly be doubted that evolution has progressed along similar lines in many, if not in all, series of the Algae. As our knowledge increases additional examples of parallelism are coming to light in the different classes, and it would seem as though in some nearly all the types of simpler plant-habit have been evolved. It is not to be expected, however, that all have been developed in every class or alternatively that all have been preserved to the present day.

THE SPECIAL STRUCTURAL FEATURES OF THE ALGAL CELL

Some of the most significant features of the algal cell are, as the earlier matter has shown, afforded by the chromatophores with their pigments and associated photosynthetic products. These vary widely in the different algal classes and are therefore more appropriately considered separately under each class.

The *resting nucleus* ((4), especially p. 213) in a large number of the Protophyta is characterised by a masking of the chromatin, so that the latter is indistinguishable from the caryolymph even after staining, and the outer nucleus appears clear and often almost homogeneous. In such cases the nucleus often possesses a large and conspicuous central nucleolus, frequently distinguished by the ready capacity with which it takes up nuclear stains (fig. 6 C, G, I, J, *k*). This has led in the past to the view that in such cases the chromatin in the resting nucleus is lodged within the nucleolus and such nucleoli have come to be styled *caryosomes*. By degrees, however, it has been shown for case after case that this assumption is incorrect, and with the demonstration by Geitler (53) that even in *Spirogyra*, which long remained as an outstanding example of a caryosome-nucleus, the nucleolus is recognisable long after the chromosomes are differentiated (fig. 10 C), the concept of the caryosome-nucleus has finally to be eliminated. Many authorities, however, still retain the term caryosome for the large and prominent nucleoli present in the nuclei of a large number of Protista. In many of the higher Algae the nucleus does not appear to differ essentially from that of archegoniate plants. Special features of the nuclei and of the process of nuclear division are dealt with under the individual classes.[1]

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[1] With reference to Hartmann's concept of monoenergid and polyenergid nuclei, see (4) p. 272, (71), (166).

Centrosomes (*centrioles*) have only been recorded in the cells of relatively few of the more advanced Algae (some Chlorophyceae, Phaeophyceae, and Rhodophyceae). Here they have usually been recognised only at times of nuclear division (fig. 6 B), although in the Bacillariophyceae (fig. 6 Q) and Sphacelariales, for example, they are often distinguishable adjacent to the resting nucleus. There is, however, good reason to believe that they are usually, if not always, present in the motile types, although here too they may not be evident except at the time of nuclear division. As regards their location there is some diversity. In what is perhaps to be regarded as the most primitive type the centrosome is located actually within the caryosome. In other cases it is situated in the outer nucleus (fig. 6 L) or in the cytoplasm in the vicinity of the nucleus (fig. 6 Q). Wherever a centrosome occurs, both in sedentary and motile forms, it plays a role in the formation of the mitotic figure, dividing into two halves which occupy the poles of the spindle (fig. 6 B). All gradations from clearly marked and deeply staining granules (cf. *Dimorpha*, fig. 244 R, p. 748) to such as are indicated only by the pronounced cytoplasmic radiations at the poles of the spindle (centrospheres) are found. The centrosomes present in the cells of sedentary Algae are perhaps to be regarded as survivals from the flagellate ancestry, since in the motile types they are usually markedly associated with the flagellar apparatus.

In the simplest case, realised in the Rhizomastigaceae (p. 750) among the colourless Flagellates (3, 75), as well as in *Chloramoeba* (p. 471), the flagella are continued backwards as a thread extending up to and into the nucleus and terminating in a centrosome located within the caryosome (fig. 6 G, H). More usually, however, the flagellar apparatus is more complex. The flagella then arise from definite, deeply staining centres, the *basal granules*, situated near the surface of the protoplast, one being usually located at the base of each flagellum (fig. 6 C, J, L, *b*). When more than one is present the basal granules are sometimes united by a delicate thread, while as a general rule a similar thread, the *rhizoplast* (28), extends from one of them (rarely from both, fig. 6 J) up to the surface of the nucleus or connects with the centrosome (fig. 6 C, L, *r*). Sometimes a number of flagella arise from a common basal granule (fig. 6 I), while in the multiflagellate zoospore of *Derbesia* the numerous flagella take their origin from two ring-shaped blepharoplasts (fig. 122 H, p. 386).[1] In *Oedogonium* (fig. 6 K) the flagella, according to Kretschmer (98), arise from two rings of separate granules.

When such motile individuals come to rest and the flagella are withdrawn or shed, both basal granules and rhizoplast disappear, to be regenerated when motility is resumed, although this has so far

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[1] It is not improbable that even in these cases there are separate granules which, owing to their proximity, have so far not been distinguished.

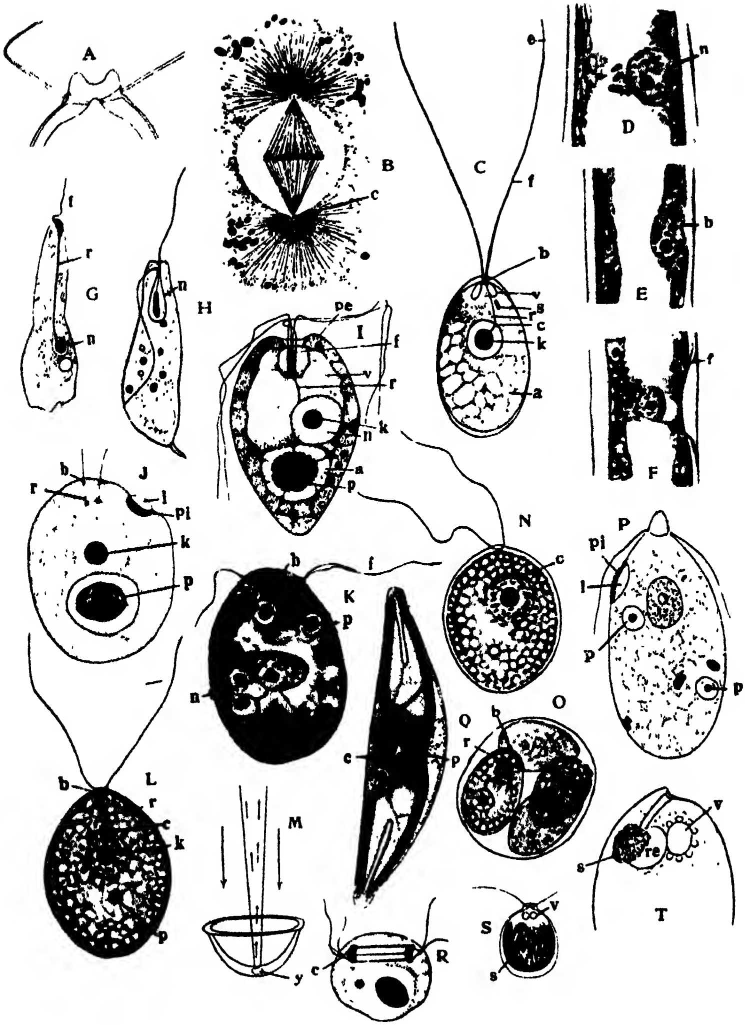
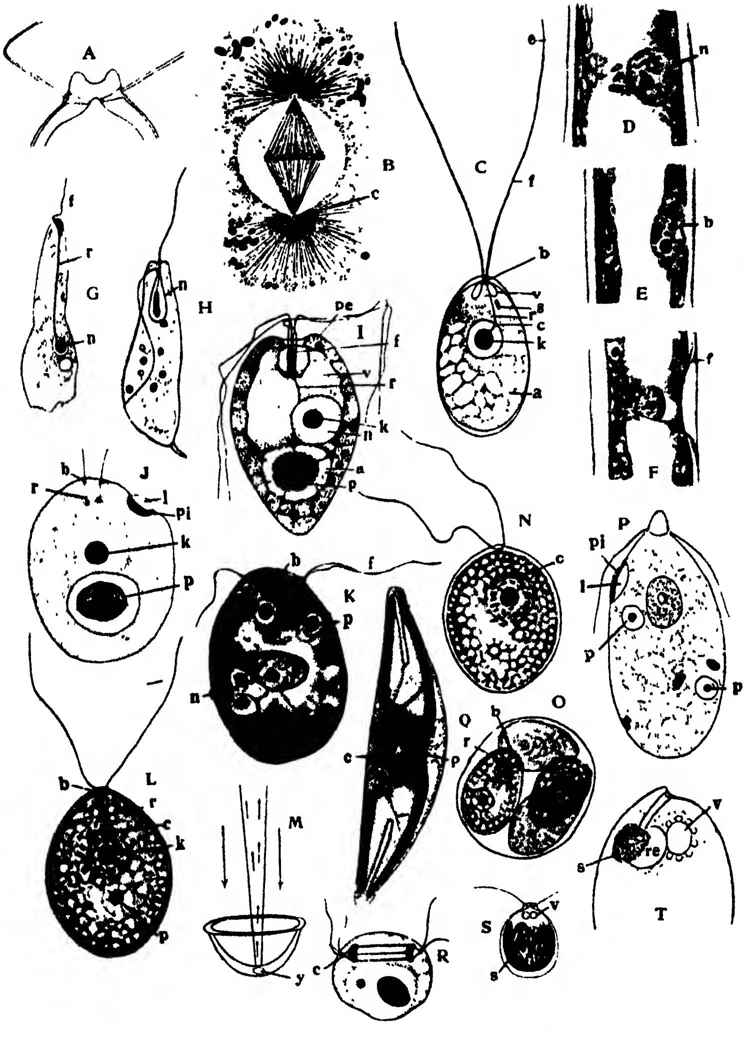


Fig. 6. A, *Sphaerella* (*Haematococcus*), emergence of flagella through membrane (after Pascher). B, *Fucus*, nuclear division (after Yamanouchi). C, *Polytoma*, showing flagellar apparatus (after Entz). D–F, *Oedogonium*, three stages in the development of the zoospore (after Kretschmer). G, *Mastigamoeba* and H, *Cercobodo*, flagellar apparatus (both after Prowazek). I, *Pyramimonas* (after Bretschneider). J, *Eudorina*, structure of single cell

only been clearly established in a few cases. According to Entz (42) in *Polytoma* and McKater (104) in *Chlamydomonas* the intranuclear centrosome then elongates to form a dumbbell-shaped body (cf. fig. 6 N) and separates into two. One of the division-products migrates through the nuclear membrane and passes through the cytoplasm to the anterior end (fig. 6 O), but the two halves remain connected by a delicate thread, identical in appearance to and no doubt homologous with the thread (centrodesmose, cf. fig. 10 S) formed between the two halves of the centrosome in the earlier phases of nuclear division (fig. 6 N). This thread constitutes the rhizoplast. The half-centrosome at the anterior end divides to form the two basal granules, one of which is connected with the rhizoplast, and from the basal granules the flagella are gradually protruded (cf. also (203)). Much the same course of events has been recorded in diverse Chrysophyceae (39), Dinophyceae (81), and Euglenineae (2), although it appears that in a considerable number of forms the rhizoplast soon disappears, so that the basal granules in later stages exhibit no connection with nucleus and centrosome.

In view of these facts the basal granules must be regarded as the equivalents of centrosomes, and in the simplest type distinguished above the intranuclear centrosome itself in fact appears to act as the point of origin of the flagella (fig. 6 G, H). The basal granules, like the centrosomes, are usually nothing more than deeply staining homogeneous bodies, but in some of the Protomastigineae (*Bodo*, *Rhynchomonas*, *Trypanosoma*, p. 750 and fig. 245 D) the flagella originate from more elaborate and prominent structures with a deeply staining central body and a surrounding zone containing little stainable matter. In view of the structural similarity of these bodies to nuclei, they have been regarded as a second nucleus essentially connected with the flagellar apparatus (kinetonucleus), and organisms possessing these structures have been grouped as Binucleatae (71). The evidence for their nuclear nature is, however, hardly satisfactory ((4) p. 275) and it may be doubted whether they represent more than an elaboration—perhaps comparable to the blepharoplasts of advanced types—of the usual mechanism for the development of flagella.

(after Mast). K, *Oedogonium*, zoospore (after Kretschmer). L, N, O, *Chlamydomonas* (after McKater); N, shows division of centrosome; O, development of rhizoplast and basal granules in daughter-individuals. M, diagram of eye-spot of Volvocales (after Mast), showing the mode of reflection of the incident light (large arrows); the small arrows indicate the beam of blue-green light reflected from the inner surface of the cup; *y*, the yellow focal spot. P, *Cladophora*, swarmer (after Strasburger). Q, *Cymbella affinis* (after Cholnoky). R, *Ochromonas*, cell-division (after Doflein). S, *Chlamydomonas reticulata* (after Goroschankin). T, *Euglena*, anterior end with vacuolar apparatus (after Klebs). *a*, starch; *b*, basal granules; *c*, centrosome; *e*, end-piece of flagellum (in C); *f*, flagella; *k*, caryosome; *l*, lens of eye-spot; *n*, nucleus; *p*, pyrenoid; *pe*, periplast (in I); *pi*, pigmentosa of eye-spot; *r*, rhizoplast; *re*, reservoir (in T); *s*, eye-spot (stigma); *v*, contractile vacuoles.



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It is possible that in some of the higher types of Algae the nuclear centrosome has been lost and that it persists merely in the form of the basal granules, but in the swarmers of a large number of these forms basal granules have so far not been recognised (cf. e.g. *Cladophora* (173, 175), fig. 6 P; *Ulva* (159); but see fig. 57 Q, p. 200). The recent establishment of such basal granules in *Oedogonium*, however, makes it probable that with modern cytological methods they will be recognised also in other types. In many cases the nucleus moves to the part of the protoplast from which the flagella arise ((175) p. 185; cf. also fig. 6 D–F). It is outside the province of this book to discuss the question whether the centrosomes are the equivalents of the blepharoplasts of archegoniate plants (76), but since both kinds of structures give rise directly or indirectly to the flagella they must be fundamentally similar. Only in the spermatozoids of the Charales do we find a body that morphologically resembles the blepharoplast of the higher plant (p. 458).

The flagella themselves are cytoplasmic prolongations which, in forms provided with a definite cell-wall (e.g. *Sphaerella*), emerge through fine pores in the membrane (fig. 6 A). Of the detailed structure of the flagella not much is known, but it is probable that they are always composed of an axial thread with surrounding cytoplasm which is contractile (94). In the coarse flagella of Euglenineae this structure is very evident. According to Korschikoff (94) the axial thread consists of a very large number of thin fibrils, whilst Dellinger (36) maintains that in *Euglena* and in some Cryptophyceae the flagella consist of a small number of fibrils spirally twisted about one another. In the Volvocales the flagella are whip-like with a thick proximal and thread-like distal portion (fig. 6 C), whilst in Xanthophyceae, Chrysophyceae, and Euglenineae some of the flagella bear numerous fine lashes (43, 150, 193, 201). According to Korschikoff (94) and Dellinger (36) these structures are artefacts.[1]

By brief treatment with a solution of silver nitrate, subsequent to drying at ordinary temperatures, Klein (91) has demonstrated in the superficial plasma of a number of Volvocales and Euglenineae (cf. also (80)) a system of fibrils appearing as fine lines connecting with the flagellar apparatus. This system of "silver lines" in the Volvocales comprises a number (2–4) of meridional ones, as well as an equatorial line and one encircling the bases of the flagella; the basal granules are connected with the meridional lines. In the colonial Volvocales these lines are stated to form a connected system occurring also in the plasmodesmae between the adjacent cells. It is suggested that they link the

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[1] Regarding the movements of flagella, see (35), (59), (99), (109), (118), and (188). For the influence of external stimuli on the movements, see (10), (16), (32), (79), (111–113), (115), (129), and (172). The terms *dikontan*, *tetrakontan*, etc. are used to indicate the number of flagella present.

flagellar apparatus of different individuals with one another. In the Euglenineae there are numerous longitudinal lines, sometimes connected by a circular one.

Apart from the flagellar apparatus the motile cells in all classes exhibit a special equipment in the possession of eye-spots (stigmata) and contractile vacuoles which in view of their wide occurrence may be considered to be an essential part of the motile habit. On the other hand, these special organelles are only rarely met with in motionless Algae, and their presence there is probably always an indication of a very close affinity to motile types. The *eye-spot* or *stigma* is to be found in most kinds of motile cells (including some colourless ones), as well as in the swarmers of the sedentary forms. It is commonly located near the anterior end (fig. 6 C, J, P) and, under a low magnification, appears as a reddish or brownish red dot or streak situated in the superficial layer of the cytoplasm ((175) p. 193, (45), (46)). Among Green and Brown Algae this eye-spot is apposed to the edge of the chromatophore or, if several are present, to one of them (cf. (17)), but in other classes it is often independent of the chromatophores (fig. 6 T). In Chrysophyceae it is commonly located at the base of the flagella (45). Its detailed structure has only been elucidated in a few cases and there is by no means general agreement.

It seems that the red pigment (in part at least haematochrome) is lodged in a thickening of the plasma-membrane, and various observers (24, 45, 159, 198) have reported its presence in the shape of droplets within a protoplasmic network. Francé (45) recorded the presence within this pigment-body of one or many, usually regularly arranged, highly refractive bodies which were stated to be of the nature of starch in Chlorophyceae and of paramylon in the Euglenineae. Neither Wager (194) nor Hamburger (70) could confirm this with reference to the Euglenineae, while later work on the eye-spots of the Volvocales (cf. below) has also failed to afford any corroboration. On the basis of the conclusions reached by Francé, Rothert ((158); cf. also (108)) suggested that the eye-spot is to be regarded as a chromoplastid. Guignard (62) showed that the eye-spot in the spermatozoids of *Fucus* originates by the modification of the chromatophore, but it may be doubted whether this structure can be justifiably called an eye-spot at all (100 *a*). There are practically no other facts that speak in favour of Rothert's view. Eye-spots do not appear as a rule to divide, but arise *de novo* in the daughter-individuals. In *Ulva*, however; Schiller (160) states that the eye-spots of the swarmers arise by the repeated division of a red-coloured mass that appears before division of the protoplast commences, each swarmer ultimately receiving one of the products. Grassé (58) also reports division of the eye-spot in *Euglena*.

The detailed work of Mast (114) on the stigma of the Volvocales indicates that here the pigment-body (*pigmentosa*) in general has a cup-shaped form (fig. 6 J, *pi*), the concavity being shallower in the unicellular than in the colonial types. The concavity is occupied by a colourless mass which in some cases at least functions as a lens and is clearly recognisable in the colonial forms (fig. 6 J, *l*) (cf. also (110), (113)), while in other cases the presence of the lens has only been inferred owing to its effect in concentrating the incident light. Both in *Cladophora* (175) (fig. 6 P) and *Ulva* (159), however, the lens is described as lying internal to the pigment-body. In the Euglenineae no certain evidence of a lens has yet been obtained (114).

Eye-spots are usually regarded as organs for the perception of light-intensity and their much greater development in the anterior individuals of the colonial Volvocales (cf. p. 99) certainly speaks in favour of this view. On the other hand, a considerable number of motile green forms are known possessing phototactic irritability in which eye-spots are apparently wanting, and Strasburger (172) already demonstrated that phototactic irritability exists in a number of colourless forms which lack eye-spots. There is no clear evidence that these forms without eye-spots are less light-sensitive than the others.

Engelmann ((41) p. 396) first showed that, if a shadow is passed from the posterior towards the anterior end along the body of an *Euglena*, there is no response until the stigma is reached, an observation that has recently been confirmed by Mast (114). Schiller ((159) p. 1700) reports that, during momentary pauses in movement, the eye-spot is nearly always directed towards the source of light.

Francé (46) believed that his lenses concentrated the light and that the pigment-body not only absorbed it but was also light-sensitive. Mast (114) has established that the region of the spectrum with maximum phototactic stimulating efficiency (the blue and green) is in general that which is most readily absorbed by the pigmentosa. He assumes that the concavity of the pigment-body is lined with a selective reflecting substance and that there is a photosensitive substance between it and the lens, the former being supposed to be connected with the flagella by a hypothetical conducting system. He finds that the pigment-body in the Volvocales is transparent for light of the longer (yellow and red) wave-lengths which come to a focus near the convex (inner) surface of the cup-shaped pigment-body, whilst the light of shorter wave-lengths (green and blue) is reflected at the outer surface of the pigment-body. These latter waves are focussed at a point between the pigment-body and the lens (cf. fig. 6 M) and then pass on in the form of a bluish green beam of relatively high intensity which can be traced for a considerable distance. Concentration by the lens and reflection at the inner surface of the cup serve to localise the illumination in the cup and to increase its intensity. The concentration of the longer waves is believed, however, to be of no significance. The photosensitive substance in *Gonium* and *Volvox* is stated to be about nine times as sensitive in the central part of the eye-spot as it is in the posterior part (116). In diverse Eugleni-

neae there is a thickening of one of the flagellar roots (fig. 240 G, p. 728) which is supposed to act as a photoperceptor and to be connected with the eye-spot.

Mast (110, 113) is of the opinion that in the Volvocales the eye-spots function as organs determining the direction of movement and that they operate in the following manner. Owing to the rotation of the colonies on their longitudinal axes the pigmentosa throws shadows which bring about rapid changes in the intensity of illumination of the photosensitive substance between it and the lens. In all of the species he examined the eye-spot in each individual of the colony is so situated that lateral illumination of the colony produces, as it rotates, alternate shading and exposure of the hyaline portion of each eye-spot, while when illuminated directly from the front or the back no such shading effect comes into operation. The lens and the reflecting substance in the cup serve to concentrate the light on the photosensitive surface, making possible more rapid and more extensive changes in luminous intensity and in the rate of absorption of light by the photosensitive substance. By lateral illumination of rotating colonies of *Volvox* he (113) was able to demonstrate that, when positive phototaxis obtains, the flagella on the momentarily illuminated side exhibit a decrease in the rate of the backward movement, while on the opposite side the rate is accelerated.

In the unicellular Volvocales the photosensitive substance is believed to be contained in the hyaline mass within the concavity of the spoon-shaped pigmentosa. In these forms there is practically no selective reflection from the concave surface of the latter and there is no evidence of a functional lens. The eye-spots are again so disposed that rotation on the longitudinal axis produces, under lateral illumination, periodic shading of the sensitive substance by the pigment-body. The eye-spots here thus function in essentially the same way as in the colonial forms, although owing to the absence of a lens and of a selective refractive surface they are probably much less sensitive.

In a number of the marine Dinoflagellata more highly differentiated bodies known as *ocelli* occur (cf. p. 685). They appear, however, to have essentially the same structure and are believed by Mast to be phylogenetically connected with eye-spots. In these ocelli the pigmentosa is often capable of amoeboid changes of shape, and a similar condition has been noted in the eye-spots of *Trachelomonas* (114).

Contractile vacuoles (101) are normally present in the motile cells of all groups of Algae. These structures do not appear, however, to occur as commonly in marine as in freshwater forms. Griessmann (60), in dealing with a number of marine Flagellates, points out that in the place of the contractile vacuoles of their freshwater allies one finds a non-contractile vacuole. Zuelzer (200) has shown that freshwater

Amoebae placed in dilute seawater that was gradually allowed to become more concentrated exhibit a slowing down of the pulsations of the contractile vacuoles which ultimately disappear; when again transferred to diluter solutions such vacuoles once more become apparent. On the other hand marine Infusoria appear usually to possess these structures, although they are absent in Rhizopods and other Protozoa of the sea.

Haye (77) distinguishes a number of diverse types of vacuolar apparatus, but in the forms here under consideration on the whole only two of these are represented. In the first, seen in many Chlorophyceae and Chrysophyceae, we have a simple vacuole which periodically contracts completely and expels its contents to the outside. Of such vacuoles there may be from one to many, but there are commonly two, pulsating alternately and lodged at the anterior end (fig. 6 C, S, *v*). In the second type of apparatus, found in Dinophyceae, Chloromonadineae, Euglenineae and some Chrysophyceae, we have a main reservoir (fig. 6 T, *re*) supplied by one or more and sometimes by a system (rosette) of secondary vacuoles (*v*), these in their turn being commonly fed by tertiary vacuoles. In this case the reservoir is periodically filled and enlarged by the complete contraction of the secondary vacuoles which may themselves be replenished by the tertiary ones; the main reservoir then slowly contracts to its original dimensions and discharges to the exterior, often through a well-defined canal. The large vacuoles or *pusules* characteristic of the Peridinieae, but so far only found in the marine forms, are of a somewhat different nature, since evident contraction does not occur (cf. p. 669).

It remains doubtful whether the simple vacuoles found in Chlorophyceae and various other classes have a definite cytoplasmic membrane which persists from one contraction (systole) to the next period of expansion (diastole). This type is known also in diverse Protozoa, and in *Amoeba* neither Haye (77) nor Day (34) could demonstrate a permanent vacuolar wall. They accept the view put forward by Taylor (183) that in such cases there is a reversible sol-gel system and that the vacuolar wall is a condensation membrane or gel disappearing with each contraction. In the second type of vacuolar apparatus, however, the reservoir possesses a definite wall which is either thin (Peridinieae) or thick and well marked (Euglenineae). Various investigators (56, 77) have shown the presence of lipoids in the wall of such vacuoles. In some cases (Peridinieae) specially differentiated cytoplasm is found around the reservoir.

The rate of pulsation depends on the rate at which water enters the cell, as well as on temperature (37, 83) and other features (151). When freshwater forms are placed in more concentrated solutions, the rate of pulsation decreases (78, 200). The usual function ascribed to the contractile vacuoles is to remove surplus water in an organism living in a hypotonic environment, but at the same time many believe in a simultaneous excretion of waste matter (34, 37) and, as a matter of fact, uric acid has been demonstrated in the vacuolar contents of *Paramoecium* (Infusoria). Adolph (1) calculated that an *Amoeba* eliminates a mass of water equal to its own body-volume in from 4 to 30 hours (cf. also (78)). There is scarcely any adequate explanation as to the *modus operandi*, although various investigators have assumed an osmotic system (37, 171), while Fortner (44) believes that ultrafiltration is involved in the filling of the vacuole.

Among the numerous other inclusions found in the protoplasts of the Algae brief reference must be made to the *mitochondria* or *chondriosomes* (spoken of collectively as the "chondriome" by the French school), although it is outside the scope of this book to deal with the many controversial matters that centre around their study. These structures appear as minute granules or not uncommonly as elongate threads (fig. 10 V, *m*) which readily stain with Janus green. Their wide distribution in Green and other Algae is undoubted (15, 33, 66, 67, 107, 120, 125, 161). Chemically they are believed to be similar to phosphatids. While many regard them as ergastic structures (i.e. products of cytoplasmic activity, perhaps connected with respiration of the protoplast), the French school in particular are largely of the opinion that they are definite organelles multiplying by division, although the evidence for this view is hardly satisfactory. They have been regarded as the bearers of the hereditary qualities of the cytoplasm (67) and in plants in particular as the primordia of the plastids (64, 65). That plastids arise from definite primordia has long been known, but it is to be doubted if they are of a comparable nature to the other structures grouped as mitochondria (31, 126). Mangenot (107) states that in the maturation of reproductive cells the chromatophores decrease in size and take on the appearance and chemical characteristics of chondriosomes and that it is from these elements that the formation of plastids in the new individuals takes place; but this also affords no proof that they should be grouped with other structures showing similar staining reactions, but not related to the plastids. Dangeard (30, 31) recognises three types of cellular inclusions which according to him are confused under the name of chondriosomes, viz. *plastidomes* giving rise to plastids, *spheromes* producing fat- and oil-globules (184), and *vacuomes* which develop into vacuoles. Guilliermond (67) holds the last of these to be quite distinct from his mitochondria.

Another little-known type of cellular inclusion in Algae are the so-called *metachromatin granules* (63, 124) which stain with nuclear stains and are believed to be identical with volutin (119). They are stated to occur in diverse Chlorophyceae, as well as in Diatoms, Euglenineae (1 *a*) and Myxophyceae. Smith ((170) p. 199) expresses the opinion that there is little to differentiate the volutin of Diatoms from the leucosin of Chrysophyceae, both of which appear as glistening rounded masses in the cells, and Gavaudan (52) also identifies metachromatin granules with the leucosin of Chrysophyceae. If, however, one compares the reactions of volutin and leucosin as enumerated for example by Molisch (122), it is evident that there are marked differences between the two substances, and in the present state of microchemical knowledge it is rash to identify outwardly similar cell-contents unless there is complete correspondence in every respect.

The normally occurring food-reserves (starch, fat, paramylon, etc.) as also the chemical characteristics and the structural features of the cell-membranes, are discussed under the diverse classes (with reference to the growth of the cell-membrane, see (26), (86), (127), (156), (162), and (199)). Various Algae afford striking evidence of growth by apposition. The staining capacity of the wall may vary greatly with the age of the cell and also changes after death (154).

THE GENERAL COURSE OF REPRODUCTION IN THE ALGAE[1]

VEGETATIVE REPRODUCTION

The processes of reproduction in the Algae may be considered under the three headings—vegetative, asexual, and sexual. We may class as *vegetative reproduction* all those processes of propagation in which portions of the plant-body become separated off to give rise to new individuals without any obvious changes in the protoplasts. Common examples are afforded by the breaking up of the threads of many filamentous Algae into short lengths (so-called *fragmentation*, cf. fig. 7 B), whereby prolific multiplication often takes place. Somewhat more specialised is the process of *hormogone*-formation met with in the filamentous Myxophyceae, where the fragments are endowed with a power of slow movement. One can include in the same category the mode of multiplication of many colonial forms by the splitting of the mature colonies into two or more parts (e.g. in *Dictyosphaerium*, *Synura*, etc.). The vegetative divisions of a *Pleurococcus*, of Desmids and Diatoms, and of many unicellular Myxophyceae are essentially of the same kind, as also is the longitudinal division of most naked flagellate forms. Many brown seaweeds (*Dictyota*, *Fucus*) propagate abundantly by the detachment of special adventitious thalli.

A more specialised type of vegetative reproduction is seen when structures are formed which are to tide over a period unfavourable for ordinary vegetative development. In these cases the cells involved undergo thickening of their membranes and at the same time plentiful

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[1] This account is to serve solely as an introduction to the main facts and to the terminology and no detailed treatment is attempted.

reserves (oil, starch) accumulate within the protoplast; in some cases special pigments are formed, so that the cells assume a distinctive (often red) tint. Such structures are called *akinetes* (196) and are most typically developed in the filamentous forms (fig. 7 G, J). Usually the cells thus modified ultimately round off more or less and separate from one another, so that each constitutes a distinct reproductive unit, but in *Cladophora* and certain other forms this is not the case and rows of cells that have assumed this character during dormant periods give rise later to new growth without falling apart. The so-called spores of Myxophyceae are likewise nothing else than specialised akinetes. The akinete is in all cases distinguished by the fact that the entire cell (including the wall) is involved in its formation.

ASEXUAL REPRODUCTION

In asexual reproduction we have, on the other hand, a rejuvenation of the protoplasts of certain cells of the alga; commonly this is associated with division of the protoplast, but whether this occurs or not the cell-contents ultimately escape from the membrane of the parent-cell (fig. 7 D–F) and give rise to a new plant. The commonest method of asexual reproduction in many classes of the Algae is by means of *zoospores*, i.e. naked flagellate protoplasts that show the distinctive features of their class (fig. 7 C, F). The first step in the development of zoospores seems in all cases to be a slight contraction of the protoplast away from the cell-wall. Only a single zoospore may be formed from the contents of each cell (*Oedogonium*, fig. 7 L, M) or, more commonly, division of the contents into two, four, eight, or more parts (fig. 7 E; several hundred in *Cladophora*, fig. 7 K) takes place and an equivalent number of zoospores is produced. In the latter case the protoplast may divide after each nuclear division (successive formation; cf. fig. 57 T, U, p. 200) or the nuclei first multiply by repeated division and then the protoplast segments into as many parts to form the swarmers (simultaneous formation; cf. fig. 40 F, G, p. 152). When zoospore-formation is accompanied by division it seems that, as a general rule, the superficial plasma-membrane and that bounding the central vacuole are not utilised in the production of the swarmers (195).

In a large number of the simpler Algae, both uni- and multicellular, the cells from which the zoospores are formed are not specially differentiated, but in *Trentepohlia* (fig. 7 I) and its allies among Chlorophyceae and in all Phaeophyceae there are special *sporangia* (fig. 7 H, *sp*) that are produced only at the times of asexual reproduction and that differ from the ordinary vegetative cells in shape and in their larger size. Liberation of the zoospores takes place in various ways that need not be considered here; in many cases at the moment of liberation the swarmers are surrounded by a delicate vesicle of a mucilaginous character (fig. 7 E, L, M), but this is of quite a temporary nature and disappears after a few seconds. In a considerable number of Algae belonging to different classes the swarmers, either after a brief period of flagellar activity or already at the time of liberation, assume an amoeboid state ((144) p. 235) and may in this condition even show holozoic nutrition.

Zoospores would appear normally to be produced at the height of vegetative activity and develop commonly during the night, to be liberated soon after daybreak. The investigations of Klebs (89) first showed that in many filamentous forms a change in external conditions acts as a stimulus to zoospore-formation, e.g. transference from flowing to still water (*Ulothrix*, *Oedogonium*), change of illumination, transference to water (in the case of terrestrial forms like *Hormidium* and *Vaucheria*), etc. Light always appears to inhibit zoospore-formation and transference to a dark place or even into diminished light-intensity often calls forth the production of swarmers. Recent investigations seem to indicate too that a certain hydrogen-ion concentration is necessary ((189); cf. also (47)).

Zoospores afford a ready means of rapid dispersal within the fluid medium at times of rich vegetative growth. They appear generally to show marked phototactic irritability, moving towards light of medium intensity, but being repelled by intense light.[1] Various Ulotrichales and Chaetophorales produce two kinds of zoospores with different phototactic sensitiveness (pp. 203, 255). The duration of movement varies within wide limits in different Algae, from half an hour up to two days or more. Towards the end of the period of movement the zoospores of most filamentous and other sedentary forms seek out dark objects upon which they come to rest. As a general rule it is the anterior end of the swarmer that becomes fastened to the substratum; this is followed by withdrawal of the flagella and the secretion of a membrane, whilst the attached end gradually broadens out into a variously shaped holdfast.

In the case of motile forms provided with cell-walls (e.g. *Chlamydomonas*) the production of new individuals by the successive division of the protoplast into two, four, or eight parts is quite of the same character, except that in this case the swarmers are usually provided with cell-walls from the time of their liberation and the naked phase is passed only within the parent-cell and is of brief duration. Of essentially the same nature is the fission of the motile naked individual of a *Chromulina*, *Euglena*, etc., which can equally well be regarded as vegetative multiplication (cf. above).

In many zoosporic forms it happens occasionally, both in nature and under conditions of culture, that, after the preliminary steps have

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[1] Cf. the literature cited in the footnote on p. 32.

occurred and the zoospores are all but formed, a rounding off of the protoplasts takes place and a cell-membrane is secreted around each (fig. 7 P, *ap*). Such structures, which are to be regarded as arrested zoospores which have skipped the motile phase, are termed *aplanospores* (196). In some cases their membranes undergo thickening, and the resulting cells, which are capable then of a prolonged resting period, are known as *hypnospores*. Under normal circumstances aplanospores are liberated sooner or later by the breaking open of the membranes of the parent-cells. If they are retained, with accompanying gelatinisation of the parent-membranes, the above-discussed *Palmella*-stages arise, which are thus merely a variant of aplanospore-formation.

In a considerable number of the Algae (e.g. many Chlorococcales; cf. p. 147) production of zoospores never takes place, but reproductive cells are formed, with or without division, by rejuvenescence of the protoplast; new cell-walls independent of those of the parent are then formed around the products, just as in aplanospore-formation. It is legitimate to suppose that in many cases at least such forms have been derived from a zoosporic ancestor, but have adopted permanently the aplanosporic condition; the evidence for this view is given in full in the later sections of this volume. All such aplanospores are to be distinguished clearly from akinetes, since the former always develop a new membrane and discard that of the parent. In many of the Algae possessing aplanospores the latter develop into absolute miniatures of the parent and acquire all its distinctive features (sculpturing of the wall, characteristic outline, etc.) whilst still enclosed in the parent-cell. In such cases it is customary to speak of *autospores* ((20) p. 108), and especially good instances are to be found in many Chlorococcales (p. 159). The term autospore can be extended even to motile individuals which acquire the mature form, etc., before liberation (e.g. *Brachiomonas*, fig. 7 O).

Of a comparable nature to aplanospores are the endospores formed in certain Myxophyceae and the tetraspores of Rhodophyceae (fig. 2 I, *d*) and Dictyotales. The *cysts*, which constitute the resting stages of most flagellate forms, are in so far peculiar that in their production a definite membrane, often not present in the ordinary vegetative condition, is secreted. That they also are comparable to aplanospores or rather hypnospores is shown by the development of similar structures in forms provided with a membrane, e.g. in *Chlamydomonas*, *Sphaerella*, and many Dinophyceae (fig. 7 N). Cyst-formation has generally been regarded as a response to unfavourable conditions, but as McKater and Burroughs ((105); cf. also (93)) have shown it often takes place when there is an abundance of nutriment.

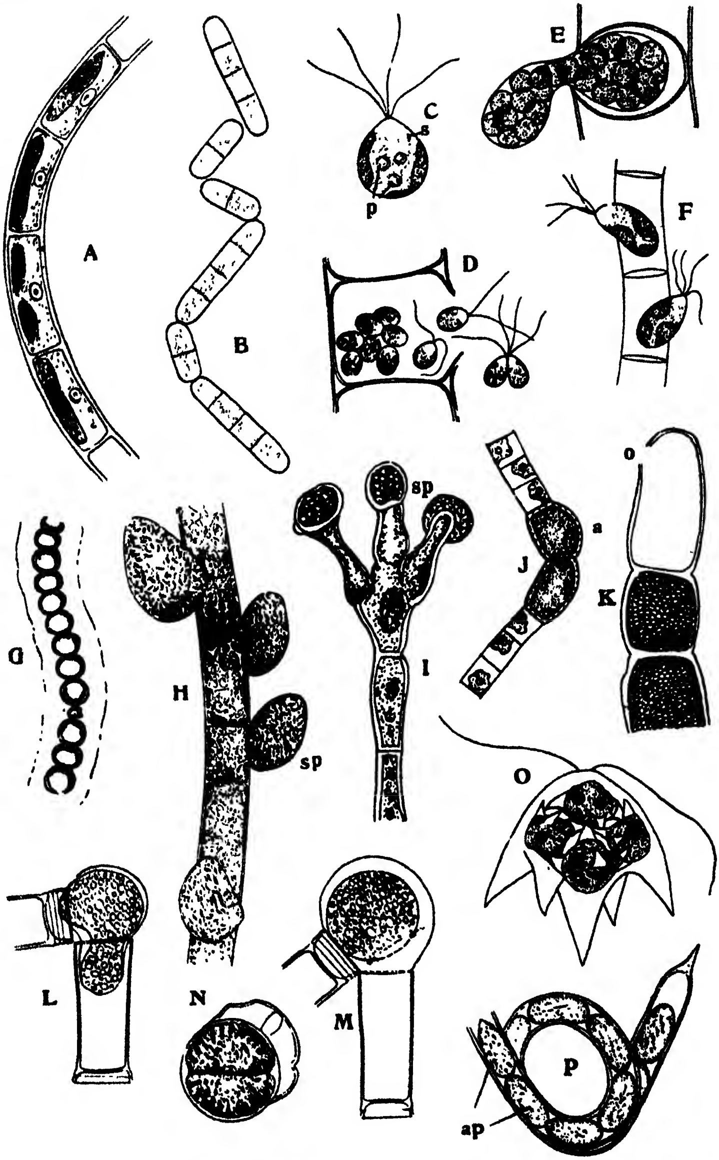

Fig. 7. Vegetative and asexual reproduction in Algae. A, B, *Hormidium* (after Klebs); A, thread; B, fragmentation of same. C–F, swarmer-formation

Sexual Reproduction

The occurrence of sexual reproduction is probably a mark of a relatively advanced stage of evolution among the simpler Algae, since such reproduction is lacking or very rare in classes that possess a relatively lowly vegetative organisation (e.g. Xanthophyceae, Chrysophyceae, Myxophyceae). Certain it is that oogamy is confined to those classes that exhibit the highest vegetative differentiation, sexual reproduction where it occurs in the others always being isogamous.

Isogamy (i.e. the fusion of morphologically identical gametes) is very usually, except among Siphonales and Phaeophyceae, combined with an absence of differentiated organs for the production of the sexual cells or gametes. In such cases the gametes arise by a division of the protoplast of the ordinary cell into a number of small bodies which are liberated in the same way as the zoospores (cf. fig. 7 D). Such gametes are in fact outwardly often only distinguishable from the latter by their smaller size, although there are sometimes differences in the number of flagella and in other details. Except in a few species of Chlamydomonadaceae the gametes are always naked[1] and they are invariably uninucleate.

Although among the simpler Algae sexual reproduction is very commonly isogamous, it has become increasingly apparent that fusion between gametes from the same parent-individual is rare; in other words the majority of isogamous Algae are dioecious.[2] The existence of two strains of individuals, long known in the isogamous Conjugales showing scalariform conjugation, was first demonstrated by Berthold(5) in the case of *Dasycladus* for the ordinary sexual fusion between motile isogametes and has since been established for many other similar cases. When the gametes from two different individuals are brought together fusion only occurs if they are of opposite sex or strain. These two strains are, however, only distinguishable by the

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[1] In *Tetraspora*, Geitler(54) records the presence of a thin membrane around the gametes, visible only after the employment of stains.

[2] This condition is often referred to as heterothallism, but in view of the wider sense which this term has assumed among Fungi, its use for isogamous Algae is misleading.

in *Ulothrix* (after West); C–E, *U. zonata*; F, *U. tenerrima*; C, zoospore; D, E, liberation of gametes; F, liberation of zoospores. G, *U. oscillarina*, akinetes (after Fritsch). H, *Ectocarpus*, unilocular sporangia (*sp*) (after Reinke). I, *Trentepohlia*, sporangia (*sp*) (after Gobi). J, *Ulothrix idiospora*, with akinetes (*a*) (after West). K, *Cladophora*, swarmer-formation (after Oltmanns). L, M, *Oedogonium*, escape of zoospore (after Hirn). N, *Glenodinium*, cyst (after Klebs). O, *Brachiomonas*, autospore-formation (after West). P, *Ophiocytium*, aplanospores (*ap*) (after Bohlin). *o*, opening through which swarmers have escaped (in K); *p*, pyrenoid; *s*, stigma.

behaviour of their gametes and it is usual therefore to speak of them as positive and negative.

Segregation into the two strains normally takes place at the time of the reduction division (cf. p. 51) and leads to the formation of equal numbers of haploid individuals of the positive and negative strains respectively. The determination of sex in these cases is *genotypic*, whereas in monoecious forms, in which the sexual cells are differentiated on the same individual in the course of its life (*Protosiphon*, *Hydrodictyon*), the determination of sex is *phenotypic* (74). Sex determination need not, however, be genotypic in all dioecious forms; in some of them asexual reproductive cells or vegetative fragments from a single individual (*Spirogyra* (27)) are able to give rise to plants of either strain, and the sex must here be determined phenotypically.

In forms with motile isogametes (whether dioecious or monoecious) big aggregates are usually formed within a few seconds when large numbers of the gametes of the two sexes are brought together in a watch-glass, and this phenomenon has been styled *clump-formation*. This feature was first recorded by Berthold (6) in *Ectocarpus siliculosus* (cf. also (73)), where each clump normally includes a central stationary female gamete and a large number of morphologically similar male gametes (fig. 8 A). In most cases, however, such clumps include numerous gametes of either sex and ultimately afford as many zygotes as there are available partners present, supernumerary gametes being apparently always of one sex (121). According to Moewus both the size of the clumps formed and their duration (i.e. degree of persistence) depend on the number of gametes of the two sexes that are present. In various isogamous species it has been established that there may occur intermediate weaker strains, whose gametes are capable of fusing with either of the normal strains (*relative sexuality* (73, 82)), behaving as a positive or a negative according to the type of gamete with which they are mixed. In such cases the sexual differentiation is clearly not as pronounced as in the normal strains. Hartmann holds the view that all sexual cells are potentially bisexual, the sex being determined by predominance of a male or female sexual potency which may result either phenotypically through the influence of external factors or genotypically through the differentiation of sex-determining genes.

There is considerable evidence that, in isogamous forms, each type of gamete secretes a specific sexual substance and that it is only when both secreta are formed that copulation occurs. This point of view was first expounded by Jollos (82) in the case of *Dasycladus*. He found that a weak positive strain could be converted into a negative one by treatment with the filtrate from a strong negative strain, and *vice versa* (cf. p. 402). Such an alteration of strain has, however, in most other cases proved to be impossible. Later Geitler (54) found that in *Tetraspora* extracts of one strain (obtained either by filtration or by the use of a centrifuge) can cause clump-formation without sexual fusion in the opposite strain and this is probably rather general. In a species of *Chlamydomonas* (*C. eugametos*) Moewus (121) has shown that the specific substances are produced only in the light, but that copulation can be induced in darkness if the respective gametes are previously treated with a filtrate[1] obtained from their own strain which has been exposed to the light. The filtrates lose their specific powers after some hours, as well as on being heated to 40–50° C. No amount of dilution of the filtrate of either strain will cause it to behave like that obtained from the opposite strain. It is therefore out of the question that there could be only a single specific substance, present in different concentrations in the gametes of the two strains, as Mainx (106) had suggested might be the case.

Pascher (146), who was the first to record clump-formation in a species of *Chlamydomonas* (*C. paupera*) where large numbers of motile gametes encircle a passive one much as in *Ectocarpus*, found that by degrees more and more of the gametes gave up their motility and constituted centres of attraction for the others. In other words they changed from effective males to effective females. On the basis of these observations he (cf. also (106) p. 506, (27)) put forward the view that the gametes at first are morphologically, but not physiologically, mature and that some time may pass before the attainment of the latter condition. Only when they are physiologically mature do they exert a chemotactic influence and attract other immature gametes. The number of attracting gametes, in proportion to the attracted, gradually increases and ultimately only mature gametes remain which have no attraction for one another. On this view there would be but a single chemotactic substance which is secreted in maximal amount only when the gametes are fully mature. Moewus (121) finds, however, that both in *Protosiphon* and in *Hydrodictyon* the residual gametes are sometimes of one and sometimes of the other strain, which is hard to harmonise with Pascher's theory and, as above stated, there is in the case of dioecious forms good evidence for the view that each strain possesses its own specific chemotactic substance.

We must therefore probably assume that in most, if not in all, cases of sexual fusion the gametes involved, even if they are not distinguished morphologically, differ in the specific chemical secretions which they produce. The secretion of analogous substances on the part of oogamous forms is highly probable (cf. especially (146) p. 574). Dangeard (29) long ago suggested an analogy between sexual fusion and holozoic nutrition, and it may well be that there exists in every

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[1] A fact that still requires explanation is that such filtrates were only found to be effective if Bacteria were present ((121) p. 488).

gamete a hunger for some substance which only the opposite strain or sex can provide. It is of interest that the specific sexual substances of one alga have no effect on the gametes of another, although closely allied species have so far not been investigated from this point of view. Isogametes are commonly positively phototactic, but after fusion the reaction changes to a negative one (cf. (106) p. 504, where the other literature is cited).

In a considerable number of isogamous Algae slight differences in the behaviour of the fusing gametes have been observed, one being more passive and the other more active (cf. fig. 8 A). This is strikingly shown in some of the Chlamydomonadaceae with gametes provided with membranes, where the one gamete receives into its protoplast the cytoplasmic contents of the other (fig. 8 J). This anisogamy (heterogamy) is more marked when the two gametes are of different sizes (fig. 8 B–D, T), the larger one in more extreme cases soon ceasing to move and awaiting passively the approach of the more active smaller one (e.g. *Chlamydomonas Braunii*, fig. 8 F, G, *Aphanochaete*, p. 264). Many isogamous forms, however, show slight differences between the sizes of the gametes without there being any regularity with respect to fusion. Thus, in *Pandorina* fusion may occur both between a small and a large gamete, as well as between two small or between two large ones (fig. 8 P, P′, P″). This state of affairs no doubt indicates a beginning of anisogamy that has, however, not yet become fixed.

In various groups of the Algae (cf. Volvocales, Ectocarpales) the anisogamy just discussed leads over quite gradually to the *oogamy* that marks the highest stage in sexual reproduction among these forms. Here the large motionless female cell or ovum is fertilised by a much smaller active male cell or spermatozoid. A simple case of this kind is found in *Chlamydomonas coccifera* Gorosch., where the female gamete is constituted by an ordinary cell which increases in size and loses its flagella, while the male cells are formed by repeated division of the contents of another individual (fig. 8 H; cf. also the case of *Chlorogonium oogamum* described on p. 113). Oogamy is, however, rare in unicellular forms and for the most part occurs in multicellular types.

In the latter, with few exceptions (*Sphaeroplea*), the sexual cells are produced in special *sexual organs* which, apart from *Chaetonema* and some Brown Algae, are always unicellular and are often very sharply differentiated from the ordinary vegetative cells. The female organ or *oogonium* (fig. 8 L, R, *o*) is usually enlarged and, except for *Fucus* (fig. 8 N) and some of its allies, invariably develops a single ovum, while the male (*antheridium*) (fig. 8 R, *a*) gives rise to one or often many male cells which are provided with flagella in all but the Rhodophyceae and are usually very active in their movements. The two kinds of sexual cells may be formed on the same (monoecism) or on different (dioecism) individuals. While the ovum is generally provided with one or more chromatophores and plentiful food-reserves (fig. 8 L, R, *o*), the spermatozoids (fig. 8 K, M) mostly contain at the best only a small inconspicuous, often yellowish chromatophore and are destitute of food-reserves; not uncommonly they are colourless.

As a general rule the ovum is retained within the oogonium, access for the fertilising spermatozoid being provided by the development of an aperture in the membrane of the female organ (fig. 8 L, R), through which at the time of maturation of the ovum a certain amount of protoplasmic slime (*sl*) is often exuded. The part of the ovum nearest the aperture commonly exhibits a colourless cytoplasmic area, the *receptive spot* (*r*), and it is here that the penetration of the spermatozoid takes place. Liberation of the ovum prior to fertilisation is characteristic of all Phaeophyceae, but among Chlorophyceae is only met with in a few cases (*Chlorogonium oogamum*, *Chaetonema*, fig. 8 Y).

All Rhodophyceae exhibit an oogamous sexual process of a very specialised kind. The spherical male cells (*spermatia*) are formed singly within the antheridia (fig. 8 O, *a*) and are invariably devoid of flagella. They are conveyed passively by water-currents to the long neck or *trichogyne* (fig. 8 I, Q, *t*) of the female organ (*carpogonium*), which in this case does not open. An open communication between the spermatium (*s*), which at this stage is enveloped by a thin membrane, and the trichogyne (*t*) is established (fig. 8 Q) and the male nucleus wanders down the neck to fuse with the female nucleus situated in the dilated base of the carpogonium.

The occurrence of sexual reproduction is usually regarded as essential for the prevention of degeneration of the race which is supposed to follow if continuous asexual or vegetative reproduction obtains, and in the more advanced types this is probably true. At the same time in many of the simpler Algae sexual reproduction never or only very rarely occurs, even in groups where certain of the members exhibit it abundantly (e.g. Desmids) Even in so relatively advanced a type as *Eudorina*, Hartmann (72) has shown the possibility of indefinite propagation by asexual means without any evidence of degeneration (cf. also (117)).

The production of sexual cells generally ensues when a considerable accumulation of nutritive materials has taken place and the climax of vegetative activity is passed (cf. (202)). Klebs (89) showed that bright light is of major importance in stimulating the production of gametes, and this conclusion has been corroborated by many other investigators and is also supported by direct observation in nature ((50) p. 67). It is probable, however, that most Algae require to be in the right state,

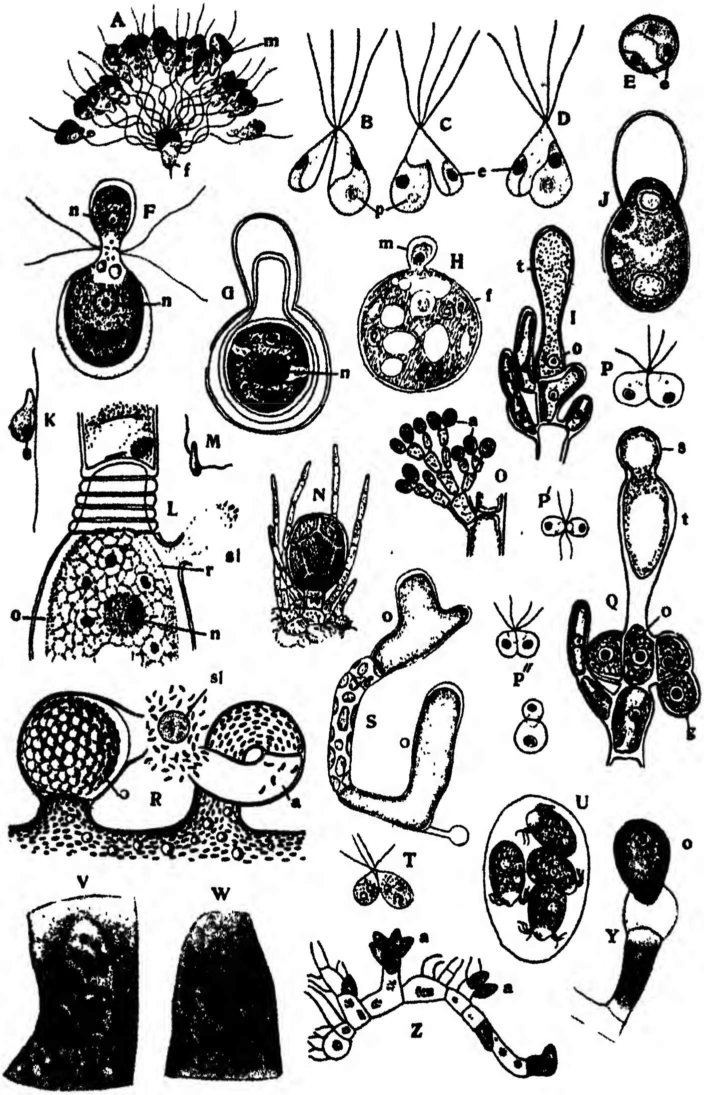

Fig. 8. Sexual reproduction among Algae. A, *Ectocarpus siliculosus*, clump-formation (after Berthold). B–E, *Enteromorpha intestinalis*, successive stages in sexual fusion (after Kylin); E, the zygote. F, G, *Chlamydomonas Braunii*, two stages in sexual fusion (after Goroschankin). H, *C. coccifera*, sexual

and that it is only when this is the case that light acts as the determining stimulus. No doubt too other factors (hydrogen-ion concentration (202), temperature, etc.) are also involved. Schreiber (163) has made it probable that in certain cases at least a deficiency of nutritive material in the environment may condition sexual reproduction (cf. also (176) p. 640). According to Transeau (186) vegetative growth must go on for a certain time before sexual reproduction is possible. He finds that in *Spirogyra* (and probably also in *Oedogonium*) the time-interval elapsing between the first appearance of a species and the commencement of sexual reproduction depends on the temperature and the specific surface (i.e. total surface divided by volume). In nature sexual reproduction in Algae usually coincides with the time of maximum abundance, and very often, though not always, it marks the end of the period of active growth and is followed by more or less complete disappearance.

In isogamous forms the fusing gametes usually become entangled by their flagella, frequently meeting end to end, although in most cases the two cells subsequently become laterally apposed to one another and it is in this position that fusion occurs (fig. 8 B–D, P, T). In a few cases a connecting strand of unknown nature has been observed joining the anterior ends of the gametes in the first stages of approximation (cf. fig. 25 I, p. 112), but it is not known whether this is of common occurrence. The product of fusion (zygote) of isogametes, usually readily recognisable by its two eye-spots, etc. (fig. 8 D, E), often continues to move for some time with the help of the flagella of the gametes from which it has been produced. Sooner or later, however, the diploid swarmer comes to rest and becomes enveloped by a membrane. In oogamous forms the secretion of a membrane takes place soon after fertilisation. Among the freshwater Chlorophyceae this membrane as a rule undergoes considerable thickening and the resulting spore (zygospore, oospore) constitutes a resting

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fusion (after Goroschankin). I, Q, *Batrachospermum moniliforme* (after Kylin); I, female organ (carpogonium); Q, the same with an attached spermatium (*s*). J, *Chlamydomonas monoica*, sexual fusion (after Strehlow). K, *Fucus*, spermatozoid (after Guignard). L, *Oedogonium Boscii*, upper half of mature oogonium (after Klebahn). M, *Vaucheria*, spermatozoid (after Woronin). N, *Fucus*, oogonium (after Thuret). O, *Chantransia corymbifera*, antheridial branch (after Kylin). P, P′, P″, *Pandorina*, sexual fusion (after Iyengar). R, *Vaucheria sessilis*, sexual organs (after Oltmanns). S. female and Z, male gametophytes of *Alaria esculenta* (after Printz). T, *Phyllobium dimorphum*, sexual fusion (after Klebs). U, *Oedogonium*, germination of oospore (after Juranyi). V, W, *Cladophora pellucida*, prophase of sporophyte (V) and gametophyte (W) (after Föyn). Y, *Chaetonema irregulare*, liberation of ovum from oogonium (after Meyer). *a*, antheridium; *e*, eye-spot; *f*, female gamete; *g*, gonimoblast; *m*, male gamete; *n*, nucleus; *o*, oogonium; *p*, pyrenoid; *r*, receptive spot; *s*, spermatium; *sl*, exudation from female organ; *t*, trichogyne.

stage in the life-cycle; the contents in these cases are laden with food-reserves and frequently harbour quantities of a yellowish red oil, the coloration in most cases probably being due to haematochrome. Chromatophores are generally not clearly recognisable in these dormant structures. Like the akinetes and hypnospores they are able to withstand prolonged desiccation and may retain their vitality over long periods (14, 164). In the vast majority of marine Algae, however, the zygote grows at once into another organism and there is no resting period.

Fusion of the cytoplasm of the gametes is accompanied by nuclear fusion which may either ensue almost immediately or be more or less appreciably delayed; in diverse Conjugales, for instance, nuclear fusion is apparently postponed until the time of germination of the zygospores (84). In many isogamous forms the chromatophores contributed by either gamete seem to persist in the zygote (fig. 8 E) (cf. e.g. (38) pp. 501, 517, (134) p. 234), although in the case of *Spirogyra*, for instance, those of the male gamete disintegrate soon after fusion (187). Korschikoff (95) reports fusion of the chromatophores in *Phyllocardium*, as also does Schiller ((159) p. 1706) in *Ulva*. In oogamous forms the chromatophore-content of the oospore is likewise entirely derived from the female cell, since the male gametes at most include but a very reduced chromatophore.

At the present time there is little evidence that the gametes of most isogamous forms can develop further in the absence of fusion, although Klebs (89) was able to induce such further development by experimental means in diverse cases (cf. also (197) p. 305) and instances are also known among Ectocarpales (6, 128). Relatively few forms will conform to the type of the *Chlamydomonas eugametos* of Moewus (121) or the *C. paupera* of Pascher (146) where every individual is a potential gamete and copulation between such individuals occurs as soon as the necessary conditions are realised, while in their absence the cells lead a vegetative existence. Among the more specialised oogamous types of Algae relatively few examples of *parthenogenesis* (development of the ovum without fertilisation) have been reported (cf. pp. 307, 460), although in various cases such parthenogenesis has been induced by experimental means (cf. (197)). Autogamy (the fusion of daughter-protoplasts or of the divided nuclei of a cell without liberation) is reported for some Diatoms (p. 631) and for diverse colourless Flagellata.

Although the meeting together of the sexual cells mostly depends on chance, the customary growth of Algae in dense communities no doubt renders sexual fusion easy of accomplishment. At the same time, since various species and genera usually occur intermingled, the production of hybrids is to be expected. That, so far, relatively little is known of hybrids among Algae is no doubt due to our imperfect knowledge of most algal species and to the lack of consecutive observation of algal forms as they occur in nature. Hybrids have been reported, for instance, among species of *Spirogyra* (p. 336) and *Fucus* (102), while Pascher (134) has successfully accomplished hybridisation between two species of *Chlamydomonas* (cf. p. 120). His methods may well give scope for a more detailed investigation of the phenomena of hybridisation in Algae.

THE LIFE-CYCLE OF THE ALGAE

Reference has already been made to the very considerable diversity in life-cycle exhibited among the Algae. Speaking broadly four main types can be distinguished.[1] The majority of the Chlorophyceae and probably all Xanthophyceae, Chrysophyceae, etc., are *haploid* organisms. That is to say the diploid condition resulting from sexual fusion is confined to the zygote itself and, when this germinates, there are two (sometimes more) successive divisions, the first of which brings about reduction in chromosome-number. Among such haploid organisms the division of the nucleus of the zygote is commonly accompanied or followed by a division of the protoplast leading to the formation of usually four asexual reproductive cells which are liberated as zoospores (fig. 8 U) or aplanospores and each of which can form a new individual. In all such haploid forms the ordinary vegetative plant is a gametophyte; in addition to reproducing by sexual means it may also exhibit abundant asexual reproduction. This latter is, however, actually an *accessory* means of reproduction and, in relation to the general course of the life-cycle, has not the same significance as the formation of asexual swarmers or other reproductive cells from the zygote which ensues after the occurrence of meiosis.

There are numerous modifications in the mode of germination of the zygote among the haploid Chlorophyceae, but the only one that need be mentioned here is that seen in *Coleochaete*, where the oospore in germination divides into 8 or 16 cells, each of which produces a swarmer (cf p. 284). A similar condition is met with among Rhodophyceae in the Bangiales and Nemalionales (*haplobiontic forms*); in the latter group the fertilised carpogonium puts forth a number of short filaments (*gonimoblasts*, fig 8 Q, *g*), some of whose cells produce motionless spores (*carpospores*) which give rise to a new thallus. In all of these cases, however, despite the more extensive development of the cell resulting from sexual fusion before it gives rise to the spores

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[1] This account of the life-cycle of the Algae is again intended merely as an introduction and a fuller discussion of these matters, combined with a consideration of other points of view, will follow in the second volume. The essential literature is to be found in (55), (57), (69), (92), (168), (178–182), (185). (57) and (71*a*) emphasise more particularly the zoological point of view.

producing the haploid plant, the first division that takes place in the zygote brings about reduction of chromosome-number.

The second type of life-cycle is of relatively restricted occurrence, being met with in a considerable number of the Siphonales (Chlorophyceae) and probably in all the Bacillariophyceae (Diatoms). In this case the ordinary individuals are *diploid* organisms and reduction occurs at the time of formation of the gametes which represent the only haploid phase. Diploid forms possibly occur also among some of the sexually reproducing Chlorococcales (cf. p. 155). The origin of this type of life-cycle is probably to be found in the prolongation of the diploid zygote stage which is not uncommon among some of the motile unicellular Green Algae (cf. especially p. 119).

The third type consists in the regular alternation of two outwardly identical individuals, the one haploid and bearing gametes, the other diploid and producing asexual spores (cf. fig. 8 V, W). Reduction occurs at the end of the diploid phase during the formation of spores and the zygote grows directly into the asexual individual. This *isomorphic* (*homologous*) *alternation*[1] is known among Chlorophyceae in the Cladophorales and the Ulvaceae, and among Phaeophyceae in the Dictyotales, *Zanardinia* (Cutleriales), and a number of other forms. It is further characteristic of all the Rhodophyceae, apart from the Bangiales and Nemalionales, but in this case there are two diploid phases alternating with the haploid one (*diplobiontic* forms). The asexual diploid individuals bear tetraspores (fig. 2 I), during the formation of which reduction occurs, and these spores give rise to a perfectly similar haploid individual bearing the sex organs; the zygote, however, in this case does not immediately give rise to the ordinary asexual individual, but with diverse complications produces gonimoblasts representing an additional diploid phase, from which carpospores are formed. It is these carpospores that grow into the diploid individual bearing the tetraspores. Attention should be drawn to the fact that isomorphic (homologous) alternation occurs in each of the three largest classes of the Algae.

The last type of life-cycle approaches that of higher plants in the fact that it exhibits an alternation of a large sporophyte and a generally small gametophyte. This *heteromorphic* (*antithetic*) *alternation* is encountered solely among Phaeophyceae, being found in a number of Ectocarpales, in *Cutleria*, in a very pronounced form in the Laminariales, and probably in a highly reduced state in the Fucales. The huge multicellular sporophytes (fig. 5 A) and the diminutive few-celled gametophytes (fig. 8 S, Z) of Laminariales present us with a succession of phases which is quite like that afforded by one of the higher archegoniate plants.

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[1] Continental workers often speak of this type of life-cycle as exhibiting antithetic alternation, but this is an incorrect use of the term.

There is considerable evidence, which will be given in full in the second volume, for the view that these diverse instances of heteromorphic (antithetic) alternation among Phaeophyceae are originally derived from an homologous alternation by gradual divergent development of the two generations (cf. also (48)). If that is the case then all true alternation among the Algae is homologous. It is perhaps not without significance that such alternation among the Green Algae is, so far as present knowledge goes, confined to isogamous forms and that all the oogamous types appear to be merely haploid. The origin of forms with homologous alternation from the haploid type must have occurred by a sudden mutation, the zygote retaining the diploid condition and, without the immediate spore-production found in the haploid types, giving rise direct to a new individual which being diploid could only reproduce asexually. This was perhaps one of the most significant steps taken in the evolution of the lower plants, since it afforded the basis for the regular alternation that characterises all the higher types.

There is, however, to be found among the Algae a clear basis for the potential origin of a true antithetic generation in the instances afforded by *Coleochaete*, Bangiales and Nemalionales (cf. above). Here we have the origin from the zygote of a contrasting type of individual which, although it is haploid, is nevertheless a distinct generation, in *Coleochaete* appearing clearly as a prolongation of the usual two divisions in the zygote of the haploid green alga. If in any one of these cases the point of reduction became shifted from the beginning to the end of this intercalated phase, we should obtain a true antithetic sporophyte, as we probably have it in the Bryophyta. Among the Nemalionales one probable case of this type has become known (*Liagora tetrasporifera*, cf. (8) p. 39), although the cytological facts are not yet elucidated, but even should this very likely instance prove to be open to another interpretation the possibility of such a shift in the point of reduction occurring would still remain. In fact, in the diplobiontic Rhodophyceae, such a change must have taken place, since the gonimoblasts that produce the carpospores in these forms are clearly homologous with those of the Nemalionales; in these Red Algae, however, the acquisition of the diploid condition by the intercalated phase has been accompanied by the development of an homologous alternation. A fuller elucidation of these points of view will be given at the end of the consideration of the Rhodophyceae. For the moment it is sufficient to have shown that among the Algae, although homologous alternation is dominant, the basis for the evolution of a true antithetic alternation also exists.

In conclusion attention may be drawn to the fact that in certain Algae complications are introduced into the life-cycle by the occurrence of special *juvenile stages* from which the normal plant arises as a vegetative outgrowth. These structures, which are directly comparable to the protonemata of Bryophyta, are met with in various Nemalionales (e.g. *Batrachospermum*), in some of the Ectocarpales, and among Chlorophyceae in the Charales.

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Class I. CHLOROPHYCEAE (ISOKONTAE).

The Algae nowadays comprised in the Chlorophyceae have long been grouped under this name. In the past, however, the Chlorophyceae also embraced a number of genera and species that have since been transferred to the Xanthophyceae (Heterokontae) (cf. p. 4). Diverse authorities have advocated a complete abolition of the name Chlorophyceae and the use in its stead of the designation Isokontae (2, 90), but there appears to be a consensus of opinion in favour of the retention of the old name for the true Green Algae, and in conformity with this the writer has abandoned his former attitude.[1] The designation Chlorophyceae, moreover, has the advantage of maintaining a uniform terminology for the classes of the Algae.

The Chlorophyceae comprise a very large number of diverse forms which enjoy a wide distribution in aquatic and terrestrial habitats. The Siphonales and Ulvaceae are almost wholly marine, while a considerable number of Volvocales, Cladophorales, and Chaetophorales occur in the sea; other groups like Conjugales and Oedogoniales are altogether confined to freshwater. As in the case of other seaweeds diverse marine Chlorophyceae (*Bryopsis*, and to a lesser extent Ulvaceae, *Cladophora*, etc.) store up considerable quantities of iodine, though it is not as definitely localised as in some Rhodophyceae (20). Many of the unicellular and colonial forms play a conspicuous rôle in freshwater plankton, whilst, apart from the Myxophyceae, no other group shows the same degree of success in a subaerial environment (31). The diversity of habit and habitat is very striking and in this respect the Chlorophyceae surpass any other algal class.

In conformity with the theory of evolution from a motile unicellular ancestry (cf. p. 3), the essential characteristics of the class are to be found in the features of the motile stages, but many of the distinctive peculiarities are equally recognisable in the sedentary phases, and even orders in which motility is lacking altogether (e.g. Conjugales) show a clear Chlorophycean stamp. These distinctive features are: (*a*) a pigmentation of the chromatophores, as far as our present knowledge goes, essentially identical with that found in the higher plants, the two chlorophylls being accompanied by only relatively small amounts of the yellow pigments; (*b*) the usual presence of pyrenoids in the chloroplasts; (*c*) the customary production of starch

[1] One can, however, scarcely agree to an inclusion of the Xanthophyceae as a subdivision of the Chlorophyceae as is done by Printz (70), since the two classes afford no evidence of any relationship (cf. also (32)).

as a food-reserve and its frequent aggregation around the pyrenoids; (*d*) the possession of cell-walls in which cellulose is usually a clearly recognisable ingredient; and (*e*) the presence in the motile phases of equal-sized and generally equally orientated flagella, usually borne at the end directed forwards during movement and commonly two or four in number. Occasional departures from this type of flagellar apparatus, met with in certain specialised forms, only seem to emphasise its remarkable uniformity in the majority.

In no other class of the Algae do we find such a striking and diverse development of those types of plant-body that must be regarded as primitive and that probably illustrate something of the innumerable attempts at the production of a soma that characterised the earlier phases of the evolution of plants. This diversity has particular interest, since the Chlorophyceae, in the pigmentation of their chromatophores and the course of photosynthesis, stand nearer to the main lines of evolution of the higher plants than any of the other algal classes. It is unnecessary to consider here the diverse development of the plant-body in the Chlorophyceae, since that will follow quite naturally in the detailed discussion of the various orders that succeeds this introductory section, and the following account deals mainly with certain general features of the class.

The Cell-wall

In view of the immense range of form within the Chlorophyceae the cell-structure naturally exhibits considerable variety. The *cell-membrane* (fig. 9 A) seems often to be composed of two or three distinct layers (85, 95), of which the innermost is usually the most conspicuous and in many cases at least consists largely of cellulose. This innermost layer, which when thickened frequently shows pronounced stratification, forms a complete envelope around the protoplast in multicellular forms and constitutes the greater part of the septa. External to the cellulose layer follows a layer of variable thickness which probably consists of pectic substances and rarely gives cellulose-reactions; it is in filamentous forms most clearly distinguishable in the longitudinal walls, but also forms the middle lamellae of the septa. Superficially the cell-membrane in certain Chlorophyceae is bounded by a cuticle, a more resistant, often sharply defined, darker layer which is, however, not chemically identical with the cuticle of higher plants and is found only on the free surface. According to Steinecke (82 *a*) the young membranes of diverse filamentous forms (*Microspora*, *Cladophora*, *Vaucheria*) consist of amyloid. In many Green Algae the membrane shows a superficial striation which has been specially studied by Correns (16) and is due to delicate folding of the lamellae of the wall.

Among the Siphonales cellulose is apparently often replaced by callose, and the membranes in this order frequently contain considerable quantities of pectin (61, 64). According to Tiffany (85) and Wurdach (95) chitin forms the outer layer of the membranes of *Cladophora* and Oedogoniales, and occurs in the middle layer of the zygospores of Zygnemaceae. Wettstein (91) suggests that, since cellulose is only recorded in the membranes of some Volvocales, whilst it appears more regularly in the more advanced Green Algae to be displaced by other substances in the Siphonales, a phylogenetic progression is indicated. Our knowledge of the chemical composition of the cell-wall in Chlorophyceae is, however, as yet so meagre and there are so many contradictory statements about it that any general conclusion can scarcely be drawn. Waren (88 *a*) has recently studied the rôle of calcium in relation to wall-formation and cell-division in the Desmid *Micrasterias*.

External to the actual membrane there are frequently present mucilaginous pectose layers which exhibit all stages between insolubility and complete solubility in water and the formation of which often appears to continue throughout the life of the alga. The resulting *envelopes of mucilage* are best developed in many Chlorococcales and Conjugales (44, 75) (fig. 9 B, C). The mode of origin of the mucilage-envelopes is in many cases by no means clear, but in Desmids there are evident and often complex pores in the walls (fig. 9 B, C, E) through which the mucus is excreted (p. 341), whilst in many cases it appears to arise by gelatinisation of the outer layer of the cell-membranes.

Incrustation with carbonate of lime (69) is of frequent occurrence in Siphonales and Charales. In the former the deposition of lime appears to take place primarily at least within the mucilaginous layers of the wall, although it may later ensue also within the other layers (14, 51, 82). In the Charales, on the other hand, the lime seems to be more of the nature of a surface-deposit and to be comparable to the not infrequent irregular deposits of crystals of carbonate of lime found on the surface of various freshwater Algae (*Vaucheria*, etc.). In many of the Siphonales the lime appears to occur in the form of arragonite ((60) p. 90). Deposits of other kinds are not uncommon, such as the iron-compounds present in the membranes of various Desmids.

THE PROTOPLAST

The protoplast usually possesses a conspicuous central *vacuole*, often traversed by cytoplasmic strands, but in many Volvocales and Chlorococcales (22) and in diverse specialised terrestrial forms (*Prasiola*, *Pleurococcus*) such large vacuoles are lacking (30, 71). According to Dangeard (21) the vacuole in the cells of the higher green forms (*Ulothrix*, *Ulva*, *Cladophora*, etc.) is replaced by numerous small ones in the swarmers which in this respect therefore also revert to the condition usual in the motile unicell.

When large vacuoles occur, as in Cladophorales and Siphonales for instance, they are bounded by a definite plasma-membrane which apparently does not divide when swarmers are produced, since the vacuole with its bounding membrane often remains behind when the swarmers are liberated (89). The sap is not uncommonly rich in tannins, but according to Tiffany (85) they are not found in the vegetative condition. The amount increases rapidly at times of sexual reproduction, although there is hardly a trace in the mature zygotes. As shown by True (87) the sap of the marine forms has an osmotic pressure higher than that of seawater; a detailed comparison between the sap of *Halicystis* and the seawater is furnished by Hollenberg (40).

Plasmodesmae are known in a number of the colonial Volvocales (fig. 9 W and p. 99), but at present at least there is no evidence of their occurrence in most of the filamentous types (cf. however (48)). The thick septa of the species of *Trentepohlia*, however, show obvious pits occupied by extensions of the protoplast (fig. 9 D), and the existence of protoplasmic connections is perhaps to be suspected here. Streaming movements of the cytoplasm are frequent.

CHLOROPLASTS AND PYRENOIDS

The *chloroplasts* (73) are well defined except in a few cases (e.g. the older cells of *Hydrodictyon*, some species of *Sphaerella*, etc.). In a very large number of the Chlorophyceae there is but a single chloroplast in each cell, the principal exceptions being found in Conjugales, Siphonales, and Charales. In the last two we find numerous small discoid or lobed chloroplasts, a type that is also occasionally met with in some of the less specialised forms (e.g. *Eremosphaera*, fig. 9 F). The chloroplasts usually lie in the lining layer of cytoplasm (i.e. they are *parietal*, fig. 9 H), but central or *axile* chloroplasts are not infrequent, being particularly common in Desmids (fig. 9 I), although not unknown in less specialised types (e.g. *Asterococcus*, *Prasiola*, fig. 9 K). Elaboration of the chloroplasts is often apparently related to increase in size of the cells, and in large-celled forms there may occur a breaking up of the single chloroplast into numerous small pieces, which still, however, retain in their entirety the typical form of the primary structure (e.g. *Cladophora*, *Sphaeroplea*).

Movement of the chloroplasts in response to varying conditions of illumination has been noted in many Chlorophyceae. Thus, in *Eremosphaera* the chloroplasts move towards the illuminated side when subjected to one-sided light, while in *Ulva* they shift from the outer to the side walls when the alga is placed in darkness (cf. also

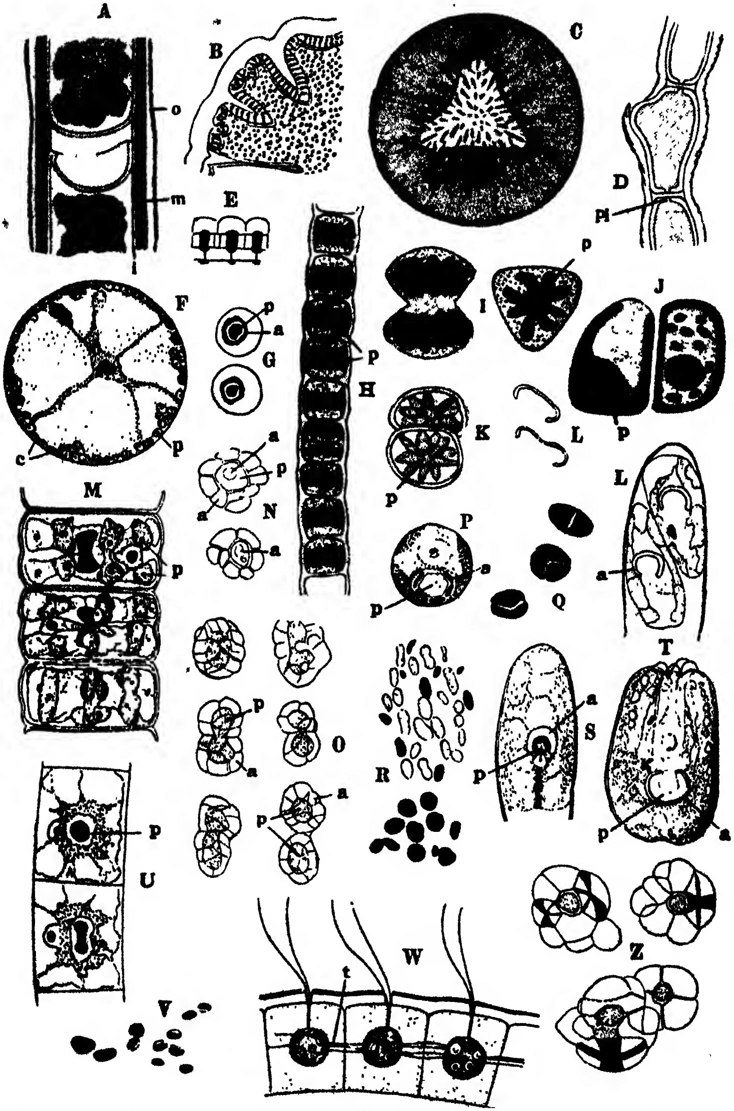

Fig. 9. Cell-structure of Chlorophyceae. A, *Cladophora*, showing the three layers of the wall (*o*, *m*, *i*) (after Brand). B, *Micrasterias*, small part of the wall showing the pores (after Schröder). C, *Staurastrum pseudofurcigerum*, pores

Mougeotia, p. 318). These movements have been specially studied by Senn (79), who believes that the chloroplasts themselves are sensitive to the light stimulus.

In the vast majority of the Chlorophyceae the chloroplasts contain *pyrenoids* (fig. 9 H–K, *p*) embedded in the substance of the chloroplast,[1] although these are regularly lacking in certain cases (e.g. *Microspora*, *Vaucheria*).[2] The pyrenoids of the Green Algae ((17), (35), (74) p. 129) are variously regarded as masses of reserve-protein and as special organs (organelles) of the cell. For the former view there speaks the fact that pyrenoids may be present or absent in closely related species and that they commonly disappear in the course of the formation of reproductive units. In such cases they slowly diminish in size till they ultimately vanish (35). Starvation also may cause a disappearance of pyrenoids, while in well-nourished cells they increase in number. Moreover, the pyrenoids in *Derbesia* ((25) p. 521) and in *Hydrodictyon* ((44a) p. 794) have been observed to dwindle or even to disappear in light of moderate intensity, but to reappear in brighter light. Dangeard (19) found that when *Scenedesmus acutus* was grown in continuous darkness the pyrenoid vanished, but it reappeared within four days after exposure to light.

In favour of the view that pyrenoids are special organs of the cell we may note their frequent great degree of persistence even under conditions of starvation, the often marked constancy in number and position, and the demonstration by Czurda ((17) p. 154) that there is

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[1] McKater (56) states that in *Chlamydomonas nasuta* the pyrenoid is situated outside the chloroplast, but this is contrary to all previous observations.

[2] Pyrenoids may also be irregular in their occurrence in one and the same species (e.g. *Debarya calospora*). Dangeard (99) reports complete disappearance of the pyrenoid in material of *Scenedesmus acutus* resuming growth after prolonged exposure to drought.

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and mucilage-envelope (after Schröder). D, *Trentepohlia*, showing pits (*pi*) in the septa (after Brand). E, *Cosmarium*, pore-organs (after Lütkemüller). F, *Eremosphaera* (after Moore). G, *Tetraspora*, two pyrenoids stained with iodine (after Czurda). H, *Ulothrix zonata* (after Klebs). I, *Staurastrum Kjelmanni* (after West), on the left the front view, on the right the end-view. J, Q, *Enteromorpha compressa*; J, double pyrenoid; Q, starch-envelopes of same (after Geitler). K, *Prasiola*, cell-structure (after Gay). L, S, *Prasinocladus* (after Zimmermann); L, outlines of pyrenoids; L′, dividing cell; S, single cell stained. M, *Hyalotheca dissiliens*, division of pyrenoid. N, *Spirogyra varians*, pyrenoids with embedded starch-grains, and O, *S. Weberi*, division of pyrenoid (both after Czurda). P, *Acanthosphaera*, pyrenoid with open starch-sheath (after Geitler). R, *Dichotomosiphon*, starch-grains (black) and chloroplasts (after Ernst). T, *Platymonas*, polar pyrenoid (after Zimmermann). U, *Zygnema pectinatum*, division of pyrenoid (after Czurda). V, *Caulerpa prolifera*, leucoplasts with starch-grains (black) (after Czurda). W, *Eudorina*, three cells showing protoplasmic connections (*t*) (after Conrad). Z, *Spirogyra setiformis*, pyrenoids with starch-sheaths in polarised light (after Czurda). *a*, grains of starch; *c*, chloroplast; *p*, pyrenoid.

a definite relation between the amount of cytoplasm and the total pyrenoid-substance in the cell. Moreover, pyrenoids often dwindle in size in resting cells (zygotes, etc.) where one would expect a storage of reserve protein, while they often multiply when there is a general removal of food-reserves and at times of active cell-division ((35) p. 142). The view put forward by Steinecke and Ziegenspeck (83) that the pyrenoids constitute ferment-receptacles is unsupported by fact (cf. also (18)).

Pyrenoids have commonly been regarded as crystalloidal in character and many writers speak of pyreno-crystals, whilst others (39, 43) have held that the crystal is embedded in a ground-mass as in the case of aleurone grains. There is no doubt, however, that the angular form of the pyrenoid is uncommon, that when it occurs the angles are not definite, that there is no double refraction, and that treatment with alcohol causes a marked contraction. In certain Conjugales (e.g. *Netrium*) the pyrenoid is an elongate rod-shaped body, betraying no crystalloidal characteristics. All these facts speak against a crystalloidal nature, as also does the frequently observed division of pyrenoids (72), and support the view put forward by Czurda ((17) p. 174) that the pyrenoid is a viscous mass of protein. The interior of the pyrenoid is invariably structureless, and the vacuoles reported by various workers have been shown to be starch-grains arising in the interior of the pyrenoid (fig. 9 N, *a*).

When a pyrenoid has attained a certain size it multiplies by division, which is a simple process of constriction (cf. fig. 9 M, O, U). Pyrenoids can, however, also arise *de novo* and, where they occur in large numbers in the cells (e.g. *Spirogyra*), both methods seem to obtain. Solitary pyrenoids usually multiply by division. Occasionally (especially in some *Spirogyras*) the cytoplasmic threads by means of which the nucleus is suspended are attached to the pyrenoids in the chloroplast (23), but since this is by no means the rule there appears to be no reason to attach special significance to it.

Compound pyrenoids[1] consisting of two pieces have been recorded by Geitler (35) in *Tetraspora lubrica*, *Dictyosphaerium pulchellum*, *Enteromorpha compressa* (fig. 9 J), etc., while pyrenoids consisting of a number of units are described by the same author in *Pyramimonas montana*, *Chlorogonium elongatum*, *Stigeoclonium*, etc. (cf. the similar structures in the Diatom *Gomphonema*, p. 596). In such compound pyrenoids the starch-envelope consists of as many pieces as there are segments in the pyrenoid and this has led to the expression of the view (35) that, wherever the starch-envelope of the pyrenoid consists of a number of separate grains, the pyrenoid is compound and comprises as many pieces as there are grains in the envelope, even if that is not discernible with present means of investigation. Czurda ((17) p. 151)

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[1] The pyrenoid of *Anthoceros* shows a similar compound character (72).

opposes this view on several grounds, in particular because pyrenoids which have temporarily lost their starch-sheath may produce a new one comprising a much larger number of grains than before.

The starch-envelope is directly apposed to the surface of the pyrenoid, and the space between the two (fig. 9 G) shown in many of the published papers on Chlorophyceae is an artefact due to shrinkage of the pyrenoid under the influence of the preservative. Chmielevsky (9) was of the opinion that the starch-grains were deposited in the superficial substance of the pyrenoid itself, while Boubier (6) believed that there was a special layer around the pyrenoid in which the starch-grains were formed, but Czurda (17) failed to find any evidence of this. The individual grains are in direct contact with one another from the first, and with few exceptions form a complete covering to the pyrenoid. As a consequence the number of grains in the envelope remains constant during their further enlargement, as well as during the growth of the pyrenoid itself. According to Czurda the individual grains of the envelope are often easily recognisable in the morning, but in the evening, after deposition during the hours of daylight, they are usually difficult to decipher. He ((17) p. 182) doubts the existence of the continuous starch-envelopes that have frequently been reported, pointing out that such would not admit of any enlargement of the pyrenoid when once laid down; such envelopes are also improbable on optical grounds.

The grains of the envelope appear to grow by apposition of layers on all sides, and their polyhedral form (giving the entire group the shape of a shell) is a result of the fact that free deposition can only take place on the external surface. It appears that during the division of a pyrenoid the two halves generally remain permanently covered by starch-grains which can only be effected by the formation of new grains in the same measure as the constriction deepens (fig. 9 O).

Chmielevsky (9) and Timberlake (86) first expressed the opinion that portions of the pyrenoid itself became detached and underwent transformation into starch-grains, and this view has been supported by a number of subsequent workers (see e.g. (3), (3 a) p. 278, (8) p. 475, (53)). The resulting grains are supposed gradually to become separated from the pyrenoids and to furnish the general stroma-starch, so that on this view all the starch of the chloroplast is derived from the pyrenoids which are supposed to produce cycle after cycle of starch-grains. The figures published in support of this view afford inadequate evidence of the asserted fact (cf. also (7), (17) p. 177), and at present this debated point cannot be regarded as settled. It is not altogether easy to suppose a transformation of protein into starch (cf. however (41)), moreover on this view there would be a marked difference between the mode of production of starch in those Green Algae that possess pyrenoids and those which lack them. The matter could probably best be settled by the observation of living material.

Pyrenoids devoid of a complete starch-sheath have been recorded in a number of cases. Such *polar pyrenoids* are known in *Acanthosphaera* (34) (fig. 9 P) and *Prasinocladus* (97) (fig. 9 L, L′, S), in both of which a part of the pyrenoid-surface is left free of starch. Of an analogous nature are the pyrenoids of *Platymonas tetrathele* (fig. 9 T), but here the pyrenoid itself shows a polar differentiation, since it is not spherical, but cup-shaped with the concavity directed anteriorily.

Starch-accumulation is usually not confined to the neighbourhood of the pyrenoids, abundant mostly larger starch-grains being deposited during active photosynthesis in the general stroma of the chloroplast. The starch-sheath of the pyrenoids possesses a greater degree of permanency than the stroma-starch which is always removed first under conditions of starvation. In certain Siphonales (*Udotea*, *Derbesia neglecta*, *Dichotomosiphon*, etc.) the starch is apparently not deposited in the discoid chloroplasts, but between them (fig. 9 R) (cf. (17), but see (25), (26)). In species of *Caulerpa* and *Udotea* Czurda ((17) p. 200) was able to demonstrate special leucoplasts which alone function in starch-formation (fig. 9 V), and it is probable that they occur also in other Siphonales. On the other hand, in the colourless members of the Volvocales (*Polytoma*, etc.) the starch-grains appear to be formed in the cytoplasm itself (67, 68). The fat-globules of *Vaucheria* and those occasionally occurring in other Green Algae appear to arise directly in the cytoplasm (84). In diverse Siphonales protein-bodies are found in the cell-sap (cf. pp. 375, 386).

As regards the pigments in the chloroplasts the little evidence that is available (62) seems to point to their general similarity with the pigments in higher green plants. According to Willstätter and Page (92) the yellow carotin and xanthophyll make up about one-third of the total pigments in *Ulva*, and there is rather more chlorophyll *b* than usual. Lubimenko (52) finds that the total amount of chlorophyll in *Ulva* and *Codium* is far less than in Phanerogams. Kylin (50) records in various Green Algae carotin and three different modifications of xanthophyll, identical with those he finds in higher plants.

Carotinoid pigments, however, also commonly occur outside the chloroplasts, especially in resting cells and in the terrestrial *Trentepohlia*, as well as in the eye-spots of motile stages (p. 33). These yellow- or red-coloured substances, known as *haematochrome*, are, according to Zopf (98) and Wisselingh (94), represented by two or more carotinoid pigments (cf. also (50)). In many cases they occur dissolved in fat-globules. Senn (80) and Geitler (33) regard them as a food-reserve. According to Pringsheim (65) the haematochrome in *Sphaerella* is formed when there is a deficiency in nitrogen (cf. also (4), (10), (59)). According to Steinecke ((82 *b*) p. 225) the frequent yellow coloration of Chlorophyceae in moorland pools is due to the abundant development of carotins in the chloroplasts as a result of nitrogen-deficiency. In *Chlorella miniata* var. *porphyrea* Boresch (5) states that he has demonstrated the presence of phycocyanin and phycoerythrin in the chloroplasts.

The Nucleus

The majority of the Chlorophyceae have uninucleate cells, but a multinucleate condition is seen in Cladophorales and probably as a preparation for the formation of reproductive units in several Chlorococcales, such as *Chlorococcum* and *Hydrodictyon*. A multinucleate condition also obtains in the Siphonales which are best regarded as unseptate multicellular individuals. Hämmerling (36), however, states that *Acetabularia mediterranea* remains uninucleate until the reproductive period, the single nucleus of the older vegetative plant being of very large dimensions and sometimes lobed (fig. 10 D).

There is little to indicate any very fundamental difference between the structure of the nucleus in the Chlorophyceae and in the higher plants.[1] In the resting condition the outer nucleus very commonly shows a great paucity of stainable substance, or at least no obvious chromatin reticulum (fig. 10 A, B, E, L); only minute grains chromatin are commonly recognisable, usually lodged at the co of a very faintly differentiated network. The nucleolus (*n*), on other hand, is usually very conspicuous in such nuclei, appearing a central caryosome (p. 28) that stains readily and deeply with nuclear stains (*caryosome-nuclei*) (cf. (1), (11), (13), (57), (58), (77), (78), (81)). The older view that in such nuclei the caryosome contained the bulk of the chromatin of the nucleus has now been practically disproved (cf. p. 28), and it appears that here also the chromatin is present in the outer nucleus but, during the interphases, occurs in a masked form which does not take up nuclear stains. Geitler (35 *a*) has shown that in *Spirogyra* the nucleolus is plainly evident at a time when the chromosomes are already well differentiated (fig. 10 C; cf. also fig. 10 N).

Judging by the available literature it would seem that the type of resting nucleus with a pronounced chromatin reticulum is only rarely found in Green Algae (49, 53). In such cases the nucleolus is usually less prominent and more than one may be present. Nuclei with a number of scattered nucleoli are found in some of the larger Desmids (46). It does not appear that the two types of nuclei are in any way characteristic of special groups, since they may occur side by

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[1] It is impossible to cite here all the literature dealing with the structure and division of the nucleus in the Chlorophyceae and only illustrative examples are chosen. The full literature is cited under the individual orders. A useful account of the older point of view is to be found in (63).

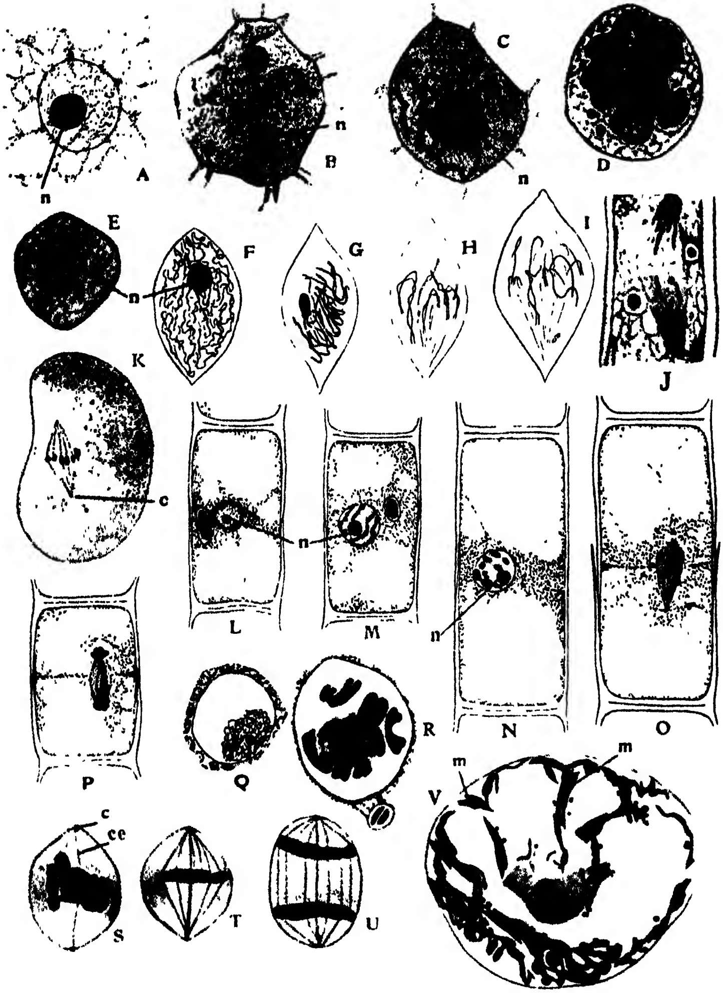

Fig. 10. Nuclear structure and nuclear division in Chlorophyceae. A, *Chlorochytrium grande*, resting nucleus (after Bristol). B, C, *Spirogyra* (after Geitler); B, resting nucleus; C, late prophase. D, *Acetabularia mediterranea*, nucleus of vegetative plant (after Hämmerling). E–J, *Oedogonium* (after Kretschmer); E, resting nucleus; F, prophase; G, late prophase; H, transition to anaphase; I, early anaphase; J, late anaphase. K, *Volvox aureus*, metaphase (after Zimmermann). L–P, *Microspora stagnorum* (after Cholnoky); L, resting nucleus; M, early prophase; N, late prophase, differentiation of chromosomes;

side in closely related genera (e.g. *Spirogyra* and *Zygnema*, p. 319). It is probable that they are not sharply distinct, but that the two types are connected by intermediate stages.

In the prophase of nuclear division chromatin-granules become increasingly conspicuous in the outer nucleus of the caryosome-nuclei and commonly become arranged to form a number of moniliform threads (fig. 10 C, M). The nucleolus at the same time generally loses its capacity to take up stains, although often persisting into late stages of the division-process (fig. 10 G, N) and in some cases it retains its full staining power for a considerable period. According to Maguitt (57) the nucleolus in *Penium* is ejected into the cytoplasm at the monaster stage and there gradually disappears. By degrees the moniliform chromatin threads contract to form the more homogeneous chromosomes (fig. 10 F, G, N). The occurrence of a spireme stage is doubtful, although recorded by some investigators. Spindles have not been observed in all cases, but that is more likely to be due to inadequate fixation than to their actual absence. Schussnig (77) is of the opinion that in *Ulothrix* the nucleolus furnishes the material for the spindle, which is here intranuclear as in many other cases (cf. fig. 10 T).

The chromosomes are commonly short rods or even mere granules (1, 11, 28, 37), and are usually not very numerous (fig. 10 N, S). Long looped chromosomes are, however, known *inter alia* in *Eremosphaera* (5[illegible]) and *Oedogonium* (47, 88, 93) (fig. 10 G–I), and in the former very numerous chromosomes have been reported. The cell-plate, where it occurs, appears as a rule to develop from the interior of the cell towards the periphery, its mode of formation being similar to that known for higher plants (54), but in a large number of Chlorophyceae cytokinesis is effected by a gradually deepening furrow. Karsten (42) has shown that in Conjugales at least nuclear division takes place prevalently at night. Amitotic division of the nucleus has been recorded in *Valonia* (27) and is well known in Charales (p. 453).

The presence of *centrosomes* has been recorded especially in Volvocales, where in the majority of cases they appear to be intranuclear ((56) and p. 29), although extranuclear centrosomes have been reported for example in *Polytomella* (55). McAllister (53), on the other hand, did not find them in *Tetraspora*. In *Chlorogonium elongatum*, according to Hartmann (38), a half-spindle is first formed at the pole of which a centrosome is recognisable; the centrosome then divides and one half

O, metaphase; P, anaphase. Q, *Codium tomentosum*, synapsis in nucleus of gametangium (after Williams). R, *Cladophora Suhriana* Kütz., diakinesis (after Schussnig). S–U, *Vaucheria sessilis* (after Hanatschek); S, early metaphase, centrosomes connected by centrodesmose (*ce*); T, annular arrangement of chromosomes at the equator of the spindle; U, anaphase. V, *Spirogyra maxima*, cell in section showing mitochondria (*m*) (after Guilliermond). *c*, centrosomes; *n*, nucleoli.

passes to the other pole, after which the other half-spindle is formed. This mode of formation of the nuclear spindle is, however, unusual, and in the majority of cases in which a centrosome occurs it divides at the commencement of nuclear division and the two halves occupy the poles of the spindle (cf. (24), (96), and fig. 10 K). Centrosomes have been recorded in *Cladophora glomerata* (76) and *Vaucheria* (37, 48) (fig. 10 S, *c*), but it remains doubtful whether they are present in most advanced Green Algae. Various investigators have, however, reported the presence of one or more granules at the poles of the spindles in the anaphase, although they were not recognised in the earlier phases ((11), (12), (77); cf. fig. 10 O).

Meiosis has so far been studied in detail in very few Chlorophyceae and, as in other plants, is characterised by the occurrence of synaptic (fig. 10 Q) and diakinesis stages (fig. 10 R).

REPRODUCTION

The methods of reproduction show great diversity. Many forms multiply largely by vegetative means; fragmentation into two or more pieces is common in colonial (e.g. *Dictyosphaerium*) and filamentous forms, while multiplication by ordinary cell-division is characteristic of *Pleurococcus* and Desmids.

Asexual reproduction by zoospores is very widespread, but such swarmers are lacking in all Conjugales, as well as in many of the Chlorococcales, while it remains doubtful whether asexual swarmers are formed in the Siphonales (apart from *Vaucheria*). In most cases the cells producing zoospores are not differentiated from vegetative cells and specialised sporangia are rare (Trentepohliaceae). The zoospores are formed either singly or frequently in some numbers from the cells; in the latter case they may arise as a result of successive division of nucleus and protoplast (*Ulothrix*) or by cleavage of the latter following on previous nuclear division (e.g. *Characium*). The zoospores are naked and possess a more or less marked colourless beak at the anterior end from which the flagella, usually two or four arise. Aplanospores (p. 41) are of frequent occurrence, both in forms normally producing zoospores (e.g. *Chlorococcum*, *Microspora*) and as a permanent development, in many genera obviously derived from zoosporic types (e.g. *Chlorella* and allied Chlorococcales).

Sexual reproduction is found widely in practically all groups except the autosporic Chlorococcales. With the exception of the latter order and the purely oogamous Oedogoniales and Charales, it is possible in each order to distinguish both isogamous forms and others showing a more or less marked degree of anisogamy, often amounting to oogamy. The latter condition has been attained by certain Chlamydomonadineae, *Cylindrocapsa*, *Sphaeroplea*, *Chaetonema*, *Coleochaete*, Oedogoniales, Vaucheriaceae, and Charales. In general the oogamous representatives of the filamentous series occupy a rather isolated position and are not easily related to the other members of their groups.

Until recently it was thought that it was characteristic of the oogamous Chlorophyceae that the ovum was invariably fertilised *in situ*, but two exceptions (*Chlorogonium oogamum*, p. 113; *Chaetonema irregulare*, p. 266) are now known in which the ovum is discharged prior to fertilisation. The product of sexual fusion, except in the Ulvaceae and Cladophoraceae with isomorphic (homologous) alternation, is almost invariably a thick-walled resting spore which sinks to the bottom of the piece of water and, if the latter dries up, may be dispersed by the wind.

Much of our recent knowledge of the details of reproduction of the Green Algae has been obtained by the method of pure culture (cf. especially (66) and p. 181). A very large proportion of the Chlorophyceae are haploid, reduction occurring in the germinating zygote and all the oogamous types show a life-cycle of this kind. Homologous alternation of two identical phases (sexual and asexual) is known in a number of Ulvaceae and Cladophoraceae, while the whole of the Siphonales, apart from the Vaucheriaceae, appear to be diploid, with reduction division occurring at the commencement of gametogenesis. Some of the Chlorococcales are possibly also diploid (cf. p. 155).

CLASSIFICATION AND STATUS OF THE CHLOROPHYCEAE

The grouping of the Chlorophyceae here adopted is based on the same principles as are followed in the classification of the remaining algal classes, and the first two orders have their parallel in most of the other classes treated in this volume. The diversity of simple filamentous forms, however, necessitates a greater degree of subdivision than is required elsewhere. It is believed that the characteristics of the Chlorophyceae are most clearly brought out, and illuminated from a comparative morphological standpoint, by considering them under the following nine orders[1] which are here briefly characterised.

I. *Volvocales.* Unicellular or colonial, either motile throughout life (Chlamydomonadineae) or forming sedentary colonies of a palmelloid (Tetrasporineae) or dendroid (Chlorodendrineae) type, the individuals of which readily revert to a motile condition. Mainly freshwater.

II. *Chlorococcales.* Unicellular or colonial, motionless in the ordinary

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[1] This is the same classification as that adopted in the second edition of *British Freshwater Algae* (90), except that the Cladophorales are treated as a separate order.

vegetative condition and either reproducing by zoospores or by aplanospores. Almost exclusively freshwater.

III. *Ulotrichales.* Filamentous, the plant-body consisting of a simple unbranched filament or cellular expanse, with small cells and a parietal (Ulotrichineae) or an axile stellate (Prasiolineae) chloroplast; or of a simple filament with large multinucleate cells (Sphaeropleineae). Most genera isogamous. A certain number marine.

IV. *Cladophorales.* Filamentous, the plant-body consisting of a simple or much branched filament with large cells containing from two to many nuclei and often elaborate chloroplasts. Most genera isogamous. Freshwater and marine.

V. *Chaetophorales.* Filamentous, plant-body heterotrichous, often sharply differentiated into prostrate and projecting systems, though the latter often reduced and the former developed as a pseudoparenchymatous discoid expanse; in many genera hairs of diverse kinds are developed, though these are not an invariable rule. Most genera isogamous. Largely freshwater.

VI. *Oedogoniales.* Filamentous, threads simple or branched, zoospores multiflagellate, oogamous; division of cells characterised by intercalation of strips of membrane between the two parts of the mother cell-wall. Exclusively freshwater.

VII. *Conjugales.* Unicellular or colonial (and then generally filamentous), or filamentous, usually with elaborate chloroplasts. No motile stages. Reproduction by cell-division and conjugation of amoeboid gametes. Exclusively freshwater.

VIII. *Siphonales.* Filamentous, the threads without septa, or vesicular, or elaborately differentiated, sometimes with a peculiar type of division (segregative division), all parts coenocytic, calcification frequent. Chloroplasts numerous and discoid. Reproduction inadequately known in many cases. but probably in the main sexual and isogamous, the Vaucheriaceae oogamous. Mainly marine.

IX. *Charales.* Plant-body markedly differentiated, with whorled arrangement of laterals of limited growth and segregation into nodes and internodes, sometimes with cortication. Chloroplasts numerous and discoid, cells normally uninucleate. Reproduction vegetative and sexual with elaborate oogonia and antheridia. Germination of zygote indirect. Freshwater and brackish.

As regards the status of the Chlorophyceae it should be emphasised that there are no evident affinities with any of the other algal classes. By contrast to the great range of simple forms, it is noticeable that the members of this class have not attained to any high degree of somatic development and, in this respect for instance, fall far short of the differentiation reached by the marine Phaeophyceae and Rhodophyceae. Indications are not lacking, however, of the existence of the potentialities for such higher development, cf. for instance *Draparnaldia* and *Draparnaldiopsis* (p. 253), the Charales (p. 447), and the Siphonales (p. 369). The opinion has been expressed ((15)

p. 8) that many of the simpler Chlorophyceae of freshwaters are reduced from forms with a higher somatic development, but no confirmation is to be obtained for this on comparative morphological grounds (cf. also (29)). There is evident a very definite upgrade development and forms, which appear advanced in vegetative features, very often also display indications of advance in their reproductive processes.

In their marked terrestrial tendency (29, 31), in their evident plasticity and capacity for development in the most diverse directions, no less than in the pigmentation of their chloroplasts and the general course of their metabolism, the Chlorophyceae stamp themselves as the descendants of the forms from which the higher green plants originated (32).

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Order I. *VOLVOCALES*

The Volvocales comprise unicellular and colonial Green Algae, either motile throughout their vegetative existence or readily resorting to the motile phase. Many of them possess a simple structure and are relatively unspecialised. They exhibit numerous points of contact among one another, so that with the continual discovery of new forms, it seems likely that the group will eventually embrace almost every conceivable modification of the simple unicellular motile organism. In no other parallel group, saving perhaps the Chrysomonadineae, is there such a bewildering diversity of simple types. The various members of the Volvocales fall more or less clearly into three suborders—the motile Chlamydomonadineae, the palmelloid Tetrasporineae, and the dendroid Chlorodendrineae.

(*a*) THE MOTILE FORMS (SUBORDER CHLAMYDOMONADINEAE)

The vast majority of the Chlamydomonadineae at present known are inhabitants of freshwater. The most usual habitats are small stagnant pools, although a number of Chlamydomonadineae occur in the plankton of lakes and several are not uncommon in that of slower-flowing rivers. Some, however, are clearly capable of existing in saline waters; thus, Artari (5) states that *Chlamydomonas Ehrenbergii* occurs in the salt lakes of the Crimea, while *Dunaliella* is normally found in concentrated saline pools in the neighbourhood of the sea. Quite a number (e.g. species of *Chlamydomonas*, *Medusochloris*, *Cymbomonas*) are truly marine, and, according to Schiller (184), Volvocales are probably abundant in marine plankton, although the colonial type appears to be very rare.

A considerable number of the freshwater forms are marked saprophytes, thriving only when photosynthesis is supplemented by organic food; this is shown by their ordinary occurrence in nature, as well as by diverse investigations of their development under cultural conditions ((5), (6), (91), (124), (193) p. 510). *Sphaerella*, however, is in the main autotrophic (165). Artari ((5) p. 463) has suggested that the Chlamydomonadaceae may be used as indicators of the degree of pollution. When abundantly represented, Chlamydomonadineae may impart a green colour to the water and some of them give it an unpleasant odour and a distinct oily taste (224). A number have been recorded from soils (17, 91, 159, 173).

Unicellular Forms

Chlamydomonadaceae. A relatively primitive type of construction is probably exemplified by some members of the genus *Chlamydomonas*[1] (fig. 11), of which, in a recent survey, Pascher ((147) p. 173) enumerates nearly 150 species. The individuals are most usually spherical or oblong in form, although other shapes (ovoid, pear-shaped, etc.) are by no means rare. The wall is mostly thin, but in a number of species (e.g. *C. gloeocystiformis*, fig. 11 D) it is differentiated into an outer firmer and an inner more mucilaginous portion (*m*), so that the protoplast appears separated by a more or less wide interval from the bounding membrane (cf. *Sphaerella*, p. 83). The membrane in the

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[1] See (30), (42), (46), (49), (72–4), (98), (226).

motile stages is stated to contain hemicelluloses, but no true cellulose ((193) p. 523).

The two equal flagella always arise anteriorily, usually from a distinct protoplasmic papilla (fig. 11 D, *b*). In some few cases this projects directly to the exterior through a narrow aperture in the membrane, but more generally such an opening is lacking and the flagella traverse very fine canals in the wall (cf. fig. 6 A). These commonly lie on either side of a more or less pronounced papilla-like thickening of the membrane (Hautwarze) (fig. 11 A, *h*) which is sometimes divided into two (fig. 11 K). The basal granules are often clearly distinguishable in young cells after suitable staining. According to Fischer (53) and Petersen (158) the flagella in *Chlamydomonas* and its allies consist of a thicker basal portion and a long thin whip-like termination (figs. 12 S, 13 C). The two contractile vacuoles[1] are, in *Chlamydomonas*, generally situated in the anterior colourless cytoplasm (fig. 11 *v*) and lie in a plane at right angles to that including the flagella (fig. 11 F), whilst the eye-spot which is sometimes lacking (or not pigmented?) is located at the side of the chloroplast (fig. 11 *e*). The latter is by far the most variable feature of the cell.

The majority of the species possess the familiar basin-shaped chloroplast with a single median pyrenoid embedded in the thick basal portion (fig. 11 A). Cells with this kind of chloroplast are found in many Volvocales, and it will be convenient in the following matter to designate this briefly as the *chlamydomonad type*. In some cases the anterior part of the chloroplast is provided with longitudinal ridges, giving a stellate outline when the chloroplast is viewed from the front end (e.g. *C. Steinii*, fig. 11 B′). In quite a number of species the pyrenoid is lateral, the chloroplast either remaining basin-shaped (*C. parietaria*, fig. 11 E) or being confined to one side of the cell (*C. mucicola*, fig. 11 G). Species of the latter type, which have been grouped as a separate genus *Chlorogoniella* (190), may show some dorsiventrality of the cell, the side not occupied by the chloroplast being more or less markedly flattened (*C. elegans*, fig. 11 I). Not uncommonly more than one pyrenoid is present. Thus a certain number of species (*Amphichloris*) are characterised by the presence of an anterior, as well as of the usual posterior pyrenoid (fig. 11 C); in such cases the anterior one usually occupies a special transverse bridge of the chloroplast which may be very massively developed (*C. pertusa* (22) p. 277) (fig. 11 J).

In other species there are a considerable number of pyrenoids scattered irregularly through the chloroplast (*C. sphagnicola* (60)) (fig. 11 K). On the other hand pyrenoids may be completely lacking (genus *Chloromonas* (226)); some species of this type have a reticulate

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[1] Wollenweber (232) has described species with four contractile vacuoles. The latter are always lacking in the marine forms.

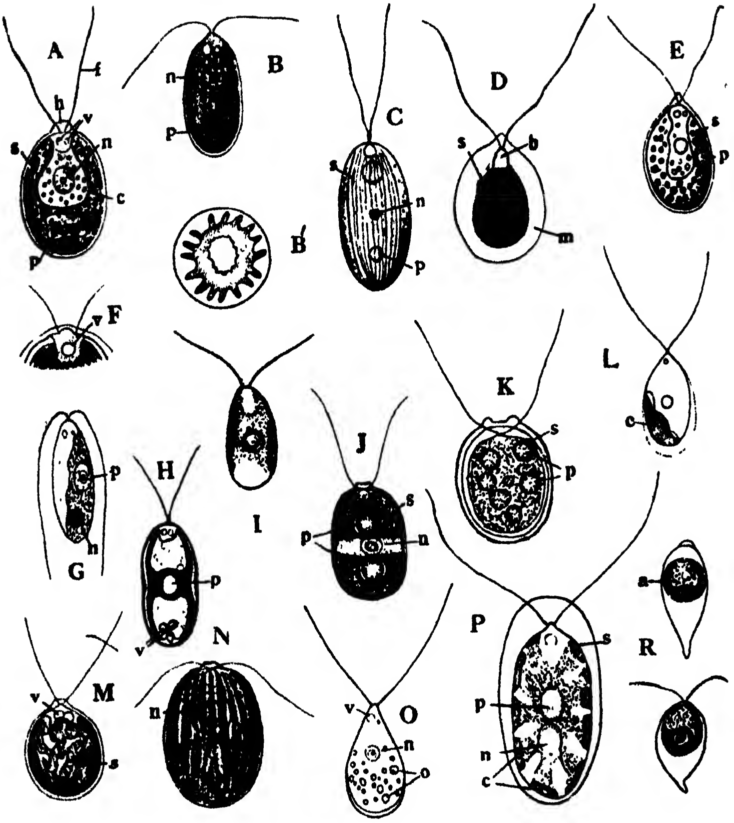

Fig. 11. Cell-structure within the genus *Chlamydomonas*. A, *C. angulosa* Dill. B, B', *C. Steinii* Gorosch.; B', optical transverse section. C, *C. Kleinii* Schmidle. D, *C. gloeocystiformis* Dill. E, *C. parietaria* Dill. F, *C. grandis* Stein, anterior end. G, *C. mucicola* Schmidle. H, *C. biciliata* Korschik. I, *C. elegans* West. J, *C. pertusa* Chod. K, *C. sphagnicola* Fritsch & Takeda. L, *C. viridemaculata* Pascher. M, *C. reticulata* Gorosch. N, *C. multitaeniata* Korschik. O, *Tussetia polytomoides* Pascher. P, *C. eradians* Pascher. R, *C. caudata* Wille, the upper individual shows an aplanospore. *a*, aplanospore; *b*, beak of protoplast; *c*, chloroplast; *f*, flagellum; *h*, Hautwarze; *m*, mucilage of wall; *n*, nucleus; *o*, oil-drops; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (A, D–F after Dill; B, H, L, O, P after Pascher; C, G after Schmidle; I after West; J, N after Korschikoff; K after Fritsch & Takeda; M after Goroschankin; R after Wille.)

chloroplast (*C. reticulata*, fig. 11 M) or numerous small discoid chloroplasts (*C. alpina* Wille). A rather exceptional type, lastly, is seen in the subgenus *Agloë* (139), where the chloroplast is H-shaped in optical section, the single pyrenoid being located in a median position in the cross-bar of the H (fig. 11 H). In *C. arachne* and *C. eradians* (fig. 11 P), which Pascher (150) regards as extreme types of this section, the chloroplast is axile and almost stellate.[1]

The single nucleus usually lies centrally or rather nearer the anterior end; in *Agloë* it is more posterior in position. According to Pascher ((147) p. 39) volutin is nearly always found in the cells of the Volvocales in the shape of rounded, highly refractive masses, commonly located near the nucleus (cf. also (212) p. 639).

The biflagellate *Chlamydomonas* is paralleled by the quadriflagellate *Carteria* (42, 49, 216) which shows analogous variations in the chloroplast. Thus, while the bulk of the species have the chlamydomonad type (fig. 12 A), the pyrenoid is lateral in *C. obtusa* Dill with a basin-shaped and in *C. Dangeardii* (fig. 12 D) with a lateral chloroplast (Dangeard's (41) genus *Corbierea*). *C. coccifera* Pascher has numerous pyrenoids, species like *C. caudata* (fig. 12 C) have none. The subgenus *Agloë* finds its parallel in the quadriflagellate *Pseudagloë*. In *C. polychloris* (fig. 12 B) there are numerous discoid chloroplasts. Several species of *Carteria* are so like species of *Chlamydomonas*, except for the different number of flagella, that a close relation between the two series of forms is undoubted. A comparison of chromosome-numbers would be of interest.

It is out of the question to describe all the numerous forms included, together with *Chlamydomonas* and *Carteria*, in the family Chlamydomonadaceae and a few examples must suffice. In Pascher's *Spiro-*

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[1] Moewus (133*a*) has demonstrated for a number of species of *Chlamydomonas* that clone-cultures in different media exhibit a considerable range of specific variability, such characteristics as shape of cell, form and degree of development of the apical papilla, and details of internal structure (shape of chloroplast, position of eye-spot, etc.) showing marked modifications. Forms appear according closely with other described species of the genus which should therefore according to Moewus' view be cancelled. As pointed out on p. 181, the fact that a given species under varied conditions of culture may assume the characteristics of some other species described from a natural habitat, cannot be regarded as a definite proof that the latter is not an independent form. While I am far from suggesting that the genus *Chlamydomonas* may not include a number of ill-founded species which should be merged in others, it would be necessary to show that such species collected in a natural habitat can by appropriate cultural methods be made to assume the characteristics of the species in which they are to be merged. When we find that such a species as *C. media*, which so reliable an observer as Klebs investigated experimentally over a considerable period without reporting any marked indications of variability, is to be merged in another with such a fluctuating character under cultural conditions, one feels inclined to doubt the validity of Moewus' conclusions.

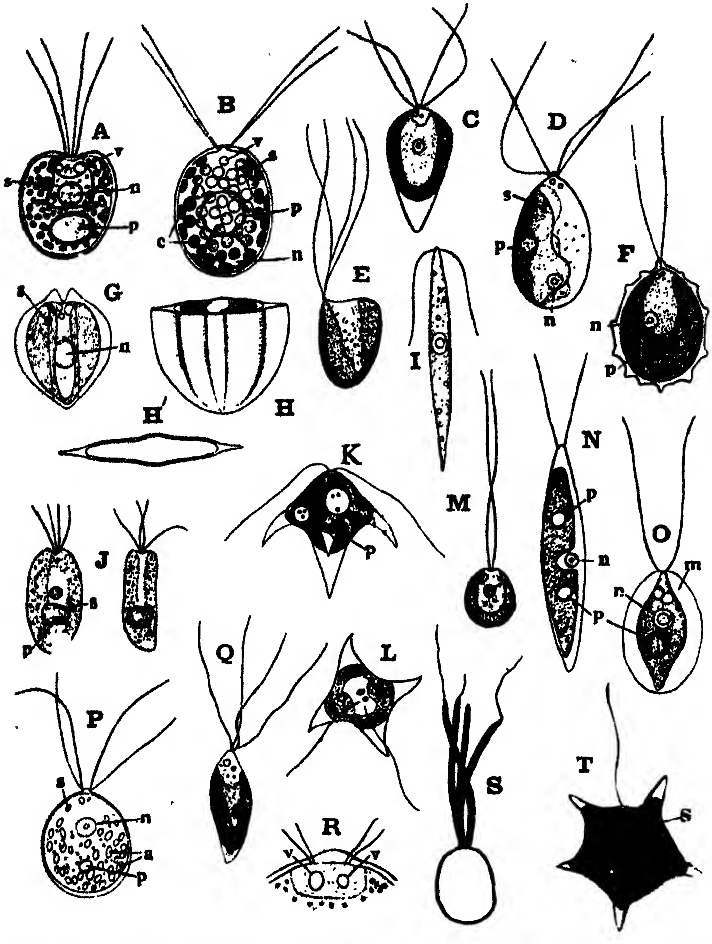

Fig. 12. Types of Chlamydomonadaceae. A, *Carteria cordiformis* (Carter) Dill. B, *C. polychloris* Pascher. C, *C. caudata* Pascher. D, *C. Dangeardii* Troitzk. E, *Cymbomonas adriatica* Schiller. F, *Lobomonas rostrata* Hazen. G, H, H', *Scherffelia phacus* Pascher; H, diagram of half an individual; H', cross-section. I, *Hyalogonium acus* Pascher. J, *Platymonas tetrathele* West, the individual on the right in side-view. K, L, *Brachiomonas Westiana* Pascher; L, the same seen from the anterior end. M, *Scourfieldia complanata* West. N, *Chlorogonium elongatum* Dang. O, *Sphaerellopsis fluviatilis* Pascher. P, *Tetrablepharis multifilis* (Klebs) Wille. Q, *Spirogonium chlorogonioides* Pascher. R, *Carteria multifilis* Fres., anterior end. S, *Carteria* sp., flagellar structure. T, *Chloroceras corniferum* Schiller. *a*, starch-grains; *c*, chloroplast; *m*, mucilage of wall; *n*, nucleus; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (A, R after Dill; B–D, G, H, P, Q after Pascher; E, T after Schiller; F after Hazen; I, O after Korschikoff; J–M after West; N after Dargeard; S after Petersen)

gonium (147) we have a fusiform *Carteria* with a slight spiral twist (fig. 12 Q). *Platymonas* (123, 223, 234), which also occurs in the sea, has a flattened cell showing some dorsiventrality, although the chloroplast is chlamydomonad in type (fig. 12 J). *Scherffelia* (33, 34, 139), likewise quadriflagellate, shows greater modifications. The cells (fig. 12 G, H) are strongly flattened and the membrane may be extended into wings at the sides of the cells, whilst at the anterior end it is produced into two wart-like outgrowths between which the four flagella arise. There are two lateral chloroplasts without pyrenoids, but they are sometimes connected by a delicate basal bridge which no doubt indicates an origin from the normal basin-shaped type. In Schiller's *Cymbomonas* ((183) p. 626, (184) p. 113) (fig. 12 E) the four flagella are inserted at one corner of the somewhat emarginate anterior end, the chloroplast being of the chlamydomonad type or segregated into a number of discs.

In the biflagellate series flattening of the cell is seen in *Scourfieldia* (215, 222) (fig. 12 M), *Phyllomonas* (110), and Pascher's *Platychloris* (147), the last a minute nannoplankton form with a tiny plate-shaped chloroplast, often more or less lateral in position and lacking a pyrenoid. Both in it and in *Scourfieldia* the flagella are of great length compared with the small dimensions of the cells. In the latter genus the posterior end is directed forwards during movement.

Lobomonas (42, 85, 110) (fig. 12 F) and *Brachiomonas* (11, 84, 221) (fig. 12 K, L) have cells which are provided with lobes or protrusions. In the former the cells are ovoid and have a relatively thick wall provided with a number of blunt solid processes. The cells of *Brachiomonas* bear one posterior and usually several anterior backwardly directed hollow horns into which the chloroplast may or may not extend. The chloroplast is not always clearly defined. *Chloroceras* (186), in which the body is likewise lobed, has only a single flagellum (fig. 12 T).

Sphaerellaceae. A rather different type of cell-structure distinguishes the forms included in the family Sphaerellaceae. The cell-wall of *Sphaerella* (*Haematococcus*)[1] (fig. 13 A, B) is strongly thickened and gelatinous and is usually traversed by simple or branched processes extending from the protoplast up to the firmer bounding layer of the membrane. The chloroplast in *S. lacustris* (fig. 13 A) is sometimes distinctly basin-shaped, though often appearing as a more or less reticulate, ill-defined, peripheral structure, provided with processes extending into the protrusions of the cytoplasm. There are commonly two pyrenoids, one anterior and the other posterior (e.g. *S. Bütschlii*, fig. 13 B), but in *S. lacustris* they are numerous and scattered. A process of the protoplast generally extends right up to the bounding membrane where the two flagella arise (fig. 13 B), but in *S. lacustris* (fig. 13 A) this is not the case and the flagella pass through canals composed of firmer substance extending through the gelatinous

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[1] See (9), (83), (157), (174), (190), (231), (237).

portion of the wall (cf. fig. 6 A). The contractile vacuoles are often numerous and apparently quite irregularly distributed near the surface of the protoplast. The cells are commonly coloured red by haematochrome in the cell-sap (92, 130, 165), its presence apparently depending largely on nitrogen-deficiency in the surrounding medium.

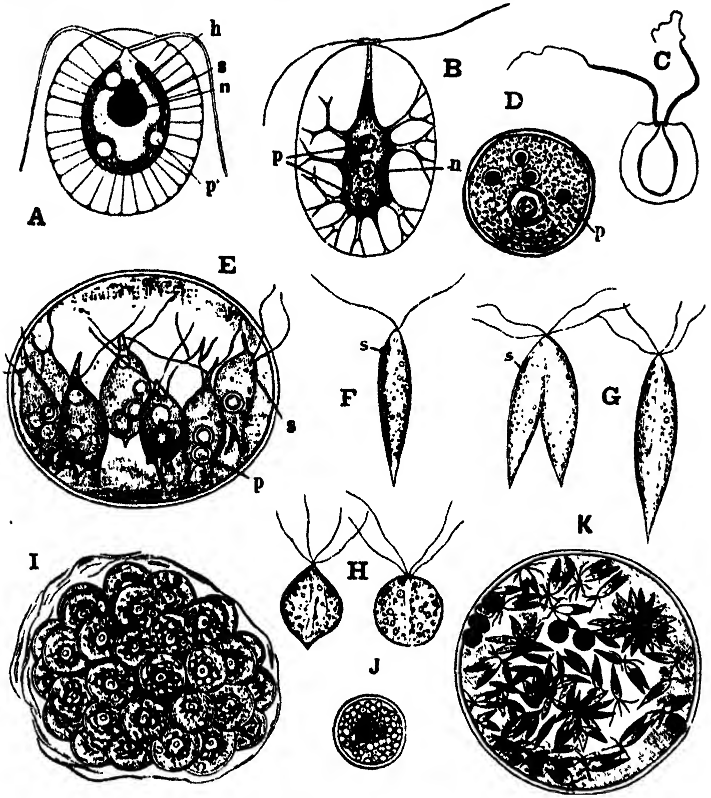

Fig. 13. Structure of the Sphaerellaceae. A, *Sphaerella lacustris* (Girod.) Wittr. B, *S. Bütschlii* Blochm. C, *Pteromonas angulosa* (Cart.) Lemm.,[1] flagellar structure. D, *Sphaerella droebakensis* Wollenweb., hypnospore. E–H, J, K, *Stephanosphaera pluvialis* Cohn; E, 8-celled coenobium; F, gamete; G, fusion of same and zygote; H, later stages of zygote; J, zygospore; K, 8-celled coenobium producing gametes, some of which are copulating. I, *Sphaerella lacustris*, palmella-stage with cysts. *h*, haematochrome; *n*, nucleus; *p*, pyrenoid; *s*, stigma. (A after Reichenow; B after Blochmann; C after Petersen; D after Wollenweber; E–H, J, K after Hieronymus; I after Wollenweber from Oltmanns.)

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[1] This is *not* one of the Sphaerellaceae.

The differences compared with Chlamydomonadaceae are sufficiently striking, but at the same time it must be realised that there is no hard and fast line of demarcation. Gelatinisation of the wall is not uncommon in species of *Chlamydomonas* (fig. 11 D) and *Carteria* (*C. Fritschii* (216)) and in Korschikoff's *Sphaerellopsis* ((110), (156) p. 278) (fig. 12 O) this is much more marked, although in other respects this genus conforms to the type of the Chlamydomonadaceae. Young individuals of *Sphaerella* may have quite a delicate close-fitting wall and are not always easily distinguished from a *Chlamydomonas*. *Chlorogonium*,[1] which has not uncommonly been referred to Sphaerellaceae, while possessing quite a thin membrane, has species (e.g. *C. euchlorum* Ehrenb.) with a parietal diffuse chloroplast containing a number of scattered pyrenoids and with numerous scattered contractile vacuoles. Other species (e.g. *C. elongatum*, fig. 12 N), however, possess only one or two pyrenoids in the chloroplast and two anterior contractile vacuoles. The elongate often almost needle-shaped form of the cells of *Chlorogonium* may be responsible for some of the peculiarities of its cell-structure. There is thus considerable likelihood that the Sphaerellaceae are to be regarded as representing a specialised type derived from the chlamydomonads ((147) p. 72).

Polyblepharidaceae. A third series of forms, the Polyblepharidaceae, are quite an artificial assemblage characterised by the absence of a cell-membrane and the faculty of change of shape of the protoplast which goes hand in hand with it. This family has in the past been regarded as primitive and as nearly allied to the unknown "flagellate" stock from which the Chlorophyceae originated, but it has become increasingly evident that this point of view cannot be maintained and that the naked character of the Polyblepharidaceous cell is to be regarded as secondary and that most of the forms in question at least are specialised rather than primitive ((147) p. 71, (58) p. 106). This is indicated by the frequent complexity of form, the common presence of unusual numbers of flagella, and the demonstration that sexuality (cf. below) is not uncommon. The number of flagella is recorded as 5–8 in *Polyblepharides* (fig. 14 A), 5 in *Chloraster* (fig. 14 K), 4 in *Pyramimonas* (fig. 14 F), *Spermatozopsis* (fig. 14 G) and *Medusochloris* (fig. 14 C), 3 in *Trichloris* (fig. 14 I), 2 in *Phyllocardium* (113) (fig. 14 O) and *Dunaliella* (fig. 14 B). In the last-named genus (7, 77, 217) and the little-known *Polyblepharides* ((39) p. 152) (fig. 14 A) the cells appear to be of the normal chlamydomonad type, those of *Dunaliella* (fig. 14 B) commonly showing a median waist and often harbouring haematochrome, which according to Labbé (119) develops especially in media of high concentration.[2] The varying number of flagella in *Polyblepharides* is possibly, as Pascher ((147) p. 89) suggests, due to

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[1] See (39) p. 114, (42) p. 79, (80), (115), (190) p. 348, (209).

[2] Sciacchitano (195) also records colourless individuals.

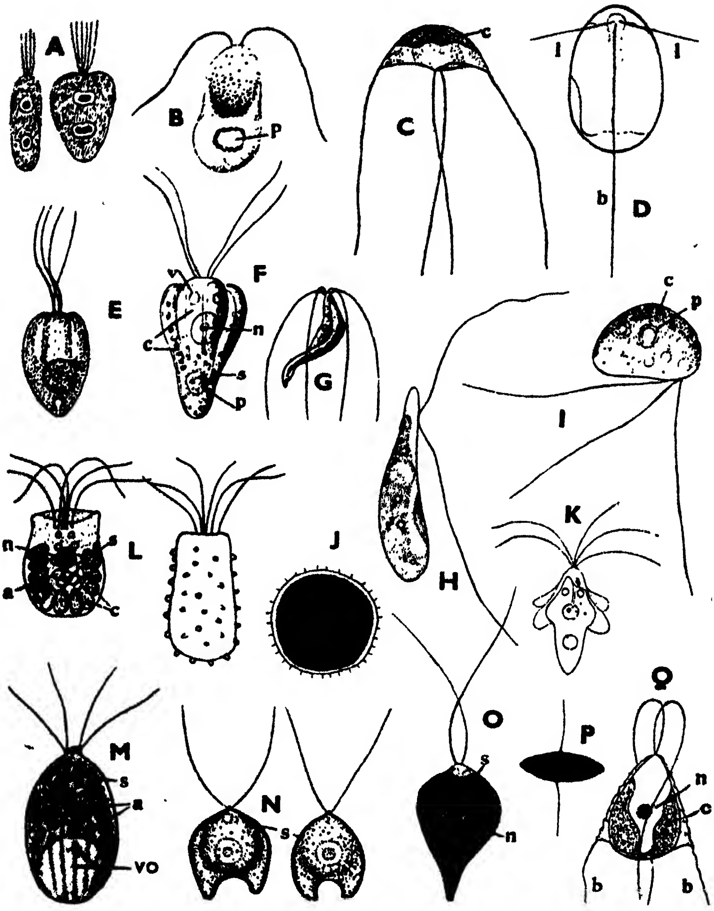

Fig. 14. Types of Polyblepharidaceae. A, *Polyblepharides singularis* Dang. B, *Dunaliella salina* Teod. C, *Medusochloris phiale* Pascher. D, I, *Trichloris paradoxa* Scherffel & Pascher; D, individual from the ventral surface; I, from the side. E, *Pyramimonas delicatulus* Griff. F, J, *P. tetrarhynchus* Schmarda; J, cyst. G, *Spermatozopsis exultans* Korschik. H, *Dangeardinella saltatrix* Pascher. K, *Chloraster gyrans* Ehrenb. L, *Pocillomonas flos aquae* Steinecke. M, *Polytomella agilis* Aragao. N, *Furcilla lobosa* Stokes. O, P, *Phyllocardium complanatum* Korschik.; P, from the anterior end. Q, *Ulochloris oscillans* Pascher. *a*, starch-grains; *b*, backwardly directed flagella; *c*, chloroplast; *l*, lateral flagella; *n*, nucleus; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole; *vo*, volutin. (A after Dangeard; B after Teodoresco; C, D, H, I, Q after Pascher; E after Griffiths; F, J after Dill; G, O, P after Korschikoff; K after Stein; L after Steinecke; M after Doflein; N after Skuja.)

their early multiplication prior to division, and this form may be actually tetrakontan. In that case *Polyblepharides* is a naked form related to *Carteria*, while *Dunaliella* is a naked ally of *Chlamydomonas*.

In *Pyramimonas* (16, 49, 65, 75) (fig. 14 E, F) the cells are inversely pyramidal or heart-shaped and more or less lobed towards the broader anterior end. The chloroplast is fundamentally basin-shaped with a median pyrenoid (*p*), but it is commonly divided into four more or less bifid lobes in front, whilst short lobes are directed posteriorily (65). *Spermatozopsis* (107) (fig. 14 G) has narrow and elongate cells curved in a sickle-shaped manner, the body at the same time exhibiting a more or less marked spiral twist; the chloroplast is a curved plate situated on the convex side of the cell and is devoid of a pyrenoid. Sometimes there are only two flagella.

The dorsiventrality evident in *Spermatozopsis* is more marked in two other genera described by Pascher. The cells of *Trichloris* ((147) p. 103) (fig. 14 I) are strongly convex on one surface, while the other is flat or faintly emarginate. The chloroplast (*c*) occupies the convex dorsal surface and is provided with two symmetrically disposed pyrenoids (*p*). The three flagella are inserted in a shallow furrow on the flat ventral surface, a little behind the bluntly rounded anterior end of the cell (fig. 14 D); two (*l*) extend out laterally on either side of the median plane, while the third (*b*) is a little longer and is directed backwards in the median line. Pascher ((147) p. 104) suggests that this third flagellum may actually be homologous with two, *Trichloris* on this interpretation being a derived tetrakontan type. He also regards *Trichloris* as a form flattened in the antero-posterior plane, the dorsal surface corresponding to the posterior end of a chlamydomonad and the flagella still occupying the morphological anterior end.

An equally remarkable type is furnished by *Dangeardinella* (151) (fig. 14 H), found in brackish pools. The elongate cells are markedly produced towards the anterior end, the two rather coarse flagella being inserted on the ventral surface a little way behind the apex. One flagellum is directed forwards and shows undulatory movements, whilst the other points backwards and remains fully extended. The chloroplast is often recognisably of the chlamydomonad type, but in most cases it is confined to the dorsal surface of the protoplast. Here the dorsal surface of the individual is produced beyond the anterior end which is represented by the point of insertion of the flagella, so that we have a further specialisation of the kind of cell seen in *Spermatozopsis*. *Dangeardinella* is of interest also owing to the formation of loose colonies (cf. p. 96).

Still greater specialisation is seen in the marine *Ulochloris* (141) (fig. 14 Q) where two of the four flagella are united to either flank of the flattened cell to constitute an undulating membrane, while the free tips of these flagella (*b*) project posteriorly. Another remarkable form is *Medusochloris* (144) (fig. 14 C), recorded from small pools in the Baltic. Here the cell has the form of a hollowed hemisphere with four processes, each bearing a flagellum at its lower edge. A lobed plate-shaped chloroplast (*c*) devoid of a pyrenoid occupies the arched convex surface. The four flagella dangle in the water like the tentacles of a *Medusa*, movement being mainly accomplished by rhythmic alterations in shape of the protoplast during which the hemispherical body alternately expands and contracts.

Steinecke's (210) *Pocillomonas* (fig. 14 L) with 5–9 (usually six) flagella arising from the emarginate anterior end, differs from other Polyblepharidaceae in possessing discoid chloroplasts (*c*) which are arranged radially in the peripheral cytoplasm of the lower part of the cell, while the central nucleus (*n*) is surrounded by a cluster of rounded starch-grains (*a*). There is no pyrenoid. The formation of starch outside the chloroplasts is remarkable.

Phacotaceae. Another artificial family is furnished by the Phacotaceae, in which the usually naked individuals are surrounded by a thick, often specially differentiated envelope, generally separated from the contained protoplast by a more or less wide space. This encapsuled type is paralleled among Chrysophyceae and Euglenineae. The envelope is mostly strongly calcified and is often brown-coloured owing to infiltration with iron-compounds. The cells have the normal chlamydomonad structure.

In *Coccomonas* (34, 209) (fig. 15 A, J) there is a cell-wall in addition to the more or less globular or angular envelope which is composed of a single piece and has a wide anterior aperture through which protrudes the papilla from the base of which the two flagella arise. The incrustation is first deposited in the form of rods or granules (fig. 15 A, *r*), but gradually spreads and ultimately forms a uniform layer. *Dysmorphococcus* (108, 110, 214) (fig. 15 I, K) is similar except for the irregular shape of the envelope and the presence of two flagellar apertures; the protoplast appears to be naked.

In the remaining Phacotaceae the envelope is markedly flattened and composed of two valves which are fitted together edge to edge like two watch-glasses; the protoplast is also usually compressed. The individuals of the common *Phacotus lenticularis* ((18), (42) p. 118, (209)) appear rounded when seen from the broad surface (fig. 15 F, H) and biconvex when viewed from the side (fig. 15 G), the edges of the valves possessing somewhat thickened rims. There is a wide space between protoplast and envelope. In *Pteromonas* (70, 196, 222, 223) (fig. 15 N–P) the envelope is broadly winged in the plane of junction of the two valves whose joined rims form a straight or slightly curved suture; the protoplast is often in close contact with the envelope at various points.

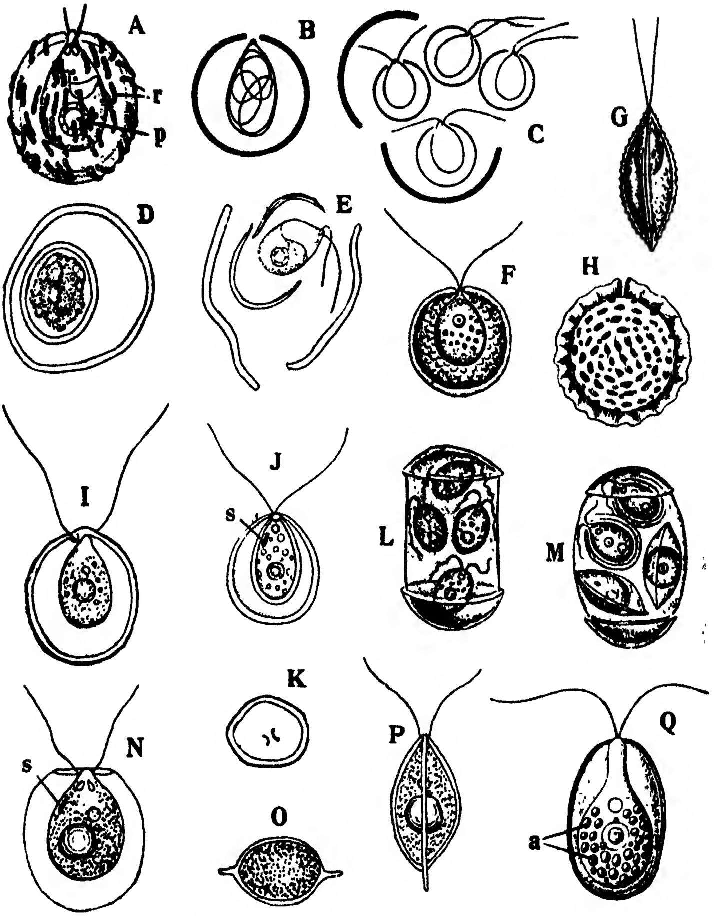

Fig. 15. Phacotaceae. A–E, J, *Coccomonas orbicularis* Stein; A, young individual showing early stage of incrustation; B, C, stages in asexual reproduction (diagrammatic); D. resting stage; E, liberation of swarmer from same. F–H, L, M, *Phacotus lenticularis* Ehrenb.; F, H, from the front; G, side-view; L, M, stages in asexual reproduction. I, K, *Dysmorphococcus variabilis* Takeda; K, from the anterior end. N–P, *Pteromonas Takedana* West; N, front-, O, end-, and P, side-views. Q, *Chlamydoblepharis brunnea* Francé. *a*, starch-grains; *p*, pyrenoid; *r*, granules of envelope; *s*, stigma. (A–E after Conrad; H after Fritsch & Rich; I, K after Takeda; N–P after West; Q after Francé; the rest after Stein.)

Colourless Unicellular Types

Pascher (147) has described a number of species of *Chlamydomonas* (*C. basistellata, C. viridemaculata*, fig. 11 L) in which the chloroplast occupies only a small part of the cell and suggests that in such cases it is in course of reduction; similar forms are stated to occur in *Carteria* ((147) p. 139). *Tetrablepharis* (228) (fig. 12 P) is a closely related colourless type in which a pyrenoid-like body (*p*) is still located in the posterior half of the cell. The common saprophyte *Polytoma* (fig. 6 C)[1] is a colourless parallel[2] to *Chlamydomonas*, lacking all trace of a chloroplast, but still producing starch in abundance, as well as volutin (96); the formation of starch commences primarily at the posterior end of the cell (167).[3] Finally in the genus *Tussetia* ((147) p. 394) (fig. 11 O) the colourless cells harbour only fat. This series of forms seems to show the manner of derivation of the numerous colourless types known among the Chlamydomonadineae, a considerable number of which, like *Polytoma*, although devoid of a chloroplast, still show the capacity to produce starch ((38) pp. 134, 203, (142)).

A few examples must suffice to illustrate the range among these colourless forms. Apart from those already mentioned which all belong to Chlamydomonadaceae, attention may be drawn to *Hyalogonium* ((147) p. 393) (fig. 12 I), a colourless parallel to *Chlorogonium*, and *Furcilla* (fig. 14 N), a genus formerly included in the Protomastigineae, a class of colourless Flagellates. *Furcilla* has flattened biflagellate cells, produced into two processes posteriorly. Skuja (205) has described a form of *F. lobosa* Stokes showing traces of a reduced chloroplast and provided with a stigma. This form is believed to be naked, but there is some doubt about this point, and it is not unlikely that *Furcilla* is a colourless member of Chlamydomonadaceae.

There are, however, quite a number of undoubted naked colourless types referable to the Polyblepharidaceae. The quadriflagellate *Polytomella* (3, 50, 51, 97) (fig. 14 M) is a naked parallel to *Tetrablepharis* (cf. fig. 12 P). *Hyaliella* (155) is very like a colourless *Dunaliella*. Both *Polytomella* and *Hyaliella* contain abundant starch, while the former also possesses an eye-spot. Pascher (155) is of the opinion that the genus *Collodictyon* (8, 19, 178), at present classed among the Protomastigineae, is another colourless member of Chlamydomonadineae

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[1] See (29), (44), (52), (54), (110), (166), (168), (171), (172).

[2] The colour is commonly yellowish which, according to Pringsheim and Mainx (168), is due to the presence of carotin and xanthophyll, although no plastids occur.

[3] Jameson (93) has described a somewhat similar form under the name of *Parapolytoma*; here, however, the front end shows an oblique emargination and the food-reserve is not starch.

which has advanced in the direction of holozoic nutrition. The same authority ((144a) p. 51) has recorded a colourless amoeboid form, *Gametamoeba*, which periodically assumes a palmelloid condition, from the spherical cells of which biflagellate gametes are produced. These give rise to the usual thick-walled zygospore of Chlamydomonadaceae. Such cases are comparable to similar ones among Chrysophyceae (p. 534) and Dinophyceae (p. 704).

Colourless types are also represented among Phacotaceae by Francé's *Chlamydoblepharis* ((54) p. 362) (fig. 15 Q), which is parallel to *Coccomonas*, and, like *Polytoma*, harbours numerous starch-grains in its protoplast.

If one surveys the diverse unicellular organisms that have been considered in the previous pages, *Chlamydomonas* emerges as a central and primitive type which not only exhibits many specialisations among its own species, but is recognisable in a more or less derived form in many of the other genera. What has above been called the normal *Chlamydomonas*-type indeed represents the most primitive green alga of which we have any knowledge. That the same type appears in a tetrakontan modification is of interest in view of the frequent occurrence of quadriflagellate swarmers in other series of the Green Algae. There is little doubt that the families Polyblepharidaceae and Phacotaceae will sooner or later have to be dismantled and their members distributed according to their true affinities.

ASEXUAL REPRODUCTION AMONG THE UNICELLULAR CHLAMYDOMONADINEAE

The ordinary method of reproduction is by simple division which always takes place along a longitudinal plane. This is most clearly apparent among the naked Polyblepharidaceae, in which separation of the protoplast into two halves is effected by a gradual constriction commencing at the back and front ends, the process of fission advancing more rapidly from the posterior pole (fig. 16 B, D). The periplast divides simultaneously with the rest of the protoplast and is gradually completed on the adjacent surfaces of the new individuals. In a dividing *Pyramimonas* or *Dunaliella* (and the same is no doubt true of other Polyblepharidaceae) the flagella are distributed among the daughter-individuals (fig. 16 A–D), each receiving half of those of the parent and forming the remainder afresh. In *Dangeardinella*, however, one daughter-individual apparently forms two new flagella, while the other retains those of the parent (151). The daughter-individuals are commonly of unequal size, very strikingly so in the genus last named.

In the forms provided with a definite cell-wall the division-process

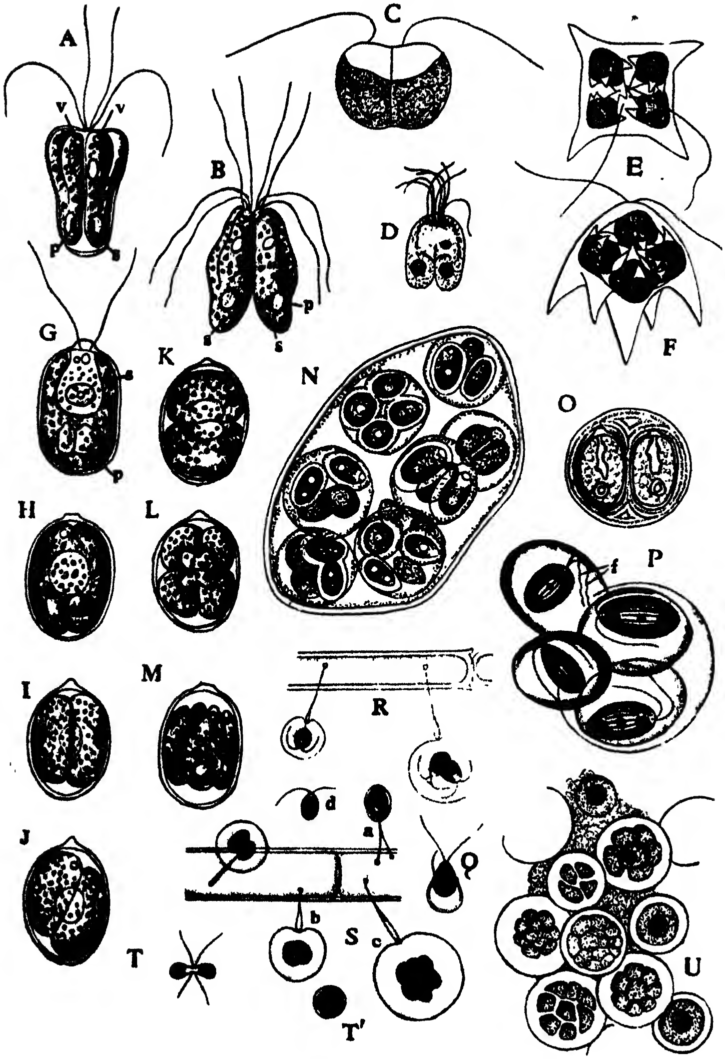

Fig. 16. Asexual reproduction of the unicellular Chlamydomonadineae. A, B, *Pyramimonas tetrarhynchus* Schmarda, successive stages of division. C, *Dunaliella salina* Teod., dividing individual. D, *Pyramimonas delicatulus* Griff., the same. E, F, *Brachiomonas Westiana* Pascher, division stages (autospores) seen from two aspects. G–M, *Chlamydomonas angulosa* Dill, successive stages of division into four. N, *C. Braunii* Gorosch., young

is somewhat modified. In the first place the new individuals always form new flagella of their own. The parent individual may remain motile during division (*Brachiomonas*, fig. 16 E, F, *Sphaerella*, *Polytoma*), but in the bulk of the species of *Chlamydomonas*, for instance, the flagella of the parent are already cast off or withdrawn prior to division. The cell-wall of the parent is likewise discarded after division and each individual secretes a new envelope. This is usually formed before liberation, but in a few cases the new individuals are at first naked ((147) p. 42).

The plane of division is always longitudinal (fig. 16 G, H), but in many cases the protoplast either during (e.g. *C. Braunii*), after (*C. angulosa*, fig. 16 J, K), or even prior to division (e.g. *Polytoma*, *Sphaerella*), rotates through a right angle (49, 135, 174), so that the plane of division comes to be transverse to the cell as a whole, although still longitudinal with reference to the protoplast. In other species (e.g. *C. gigantea*), however, no such rotation takes place. When it occurs, it is clearly evident in the altered position of the stigma and contractile vacuoles. The first division is commonly followed by a second which ensues in a plane at right angles to the first, but again longitudinal to the axis of the protoplasts formed in the first division (fig. 16 L, M). More rarely division into eight or sixteen parts is observed, but even these later divisions always run longitudinally with respect to the dividing protoplasts. When division is completed, the daughter-individuals commonly become ranged parallel to one another within the distended parent-membrane (fig. 16 M). According to Reichenow (174) and Pascher ((147) p. 43) rotation of the protoplast during division to the transverse plane occurs mainly in forms with narrow elongated cells.

In *Brachiomonas* (fig. 16 E, F) the new individuals acquire the characteristic shape of the parent before liberation, a fact which although not so striking in other cases is equally true of the majority of Chlamydomonadineae with cell-membranes. Among the Phacotaceae, where division into four appears to be the rule (fig. 15 B, C, L, M), the daughter-individuals likewise form a new envelope and flagella prior to liberation from the parent. In this respect the encapsuled Chlamydomonadineae differ from the corresponding forms among the Chrysophyceae and Euglenineae.

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palmelloid stage. O, *C. Franki* Pascher, the same. P, *C. Kleinii* Schmidle, the same. Q–T, *Physocytium confervicola* Borzi; R, two individuals with swarmers; S, individuals in various stages of development (*a*–*c*) and a gamete (*d*); T, sexual fusion; T , zygote; Q, germination of same. U, *Chlamydomonas truncata* Fritsch & Rich, palmella-stage. *f*, flagella; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (A, B, G–M after Dill; C after Teodoresco; D after Griffiths; E, F after West; N after Goroschankin; O after Frank; P after Schmidle; Q–T after Borzi; U after Fritsch & Rich.)

As regards the details of division, the chloroplast always appears to be halved longitudinally and, when there is a single pyrenoid, it usually broadens and separates into two halves with the chloroplast (fig. 16 A, G). If several pyrenoids are present, these are apportioned among the daughter-cells. In some cases, however, the pyrenoid disappears during division and is formed *de novo* in the resulting daughter-individuals ((38) p. 171, (80)). The behaviour of stigma and contractile vacuoles is not clear, but it seems that in the case of the former one daughter-cell receives the stigma of the parent, whilst that of the other is formed afresh. It is not improbable, however, that even the individual retaining the parent stigma later forms a new one, since after division cells with two stigmata are not uncommon (cf. (147) p. 45).

PALMELLOID AND OTHER SEDENTARY PHASES

In various Chlamydomonadineae the asexual division process, under certain not clearly established conditions,[1] is modified through the failure of the daughter-cells to develop flagella and a progressive gelatinisation of the membranes of the successive generations (4, 72, 101). The resulting "*Palmella*-stages" often attain to considerable dimensions and vary in appearance, according as the mucilage is diffluent or the strata formed by the successive mother-cell membranes remain distinct (*Chlamydomonas Braunii*, fig. 16 N). The cells of such palmelloid phases commonly exhibit contractile vacuoles and eye-spots. In the majority of cases these stages are only observed occasionally and are probably of brief duration, but in some species (e.g. *C. Kleinii*, fig. 16 P) they become the dominant condition. The case of *C. Kleinii* is, moreover, of special interest, because the cells retain their flagella and may even exhibit slight movements within the mucilage (188). In all cases the individuals in these palmelloid phases readily develop flagella and return to the motile condition.

A relatively simple condition is seen in *C. Franki* Pascher (55), where the individuals occasionally develop a thick stratified gelatinous membrane, with loss of flagella, and may exhibit a few divisions in this condition before they are again liberated as motile cells (fig. 16 O). Such a case appears as a mere extension of the habit of dividing after cessation of motility that characterises many Chlamydomonadineae, especially when such division is accompanied by the secretion of a certain amount of mucilage about the dividing cell ((147) p. 55). From the *Palmella*-stages it is only a slight step to the Algae grouped as Tetrasporineae (p. 121), in which motility is confined to the repro-

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[1] According to Vischer (220) the formation of palmelloid stages in *C. pulvinata* is favoured by liquid media and the presence of ions that tend to cause swelling. Frank ((55) p. 24) found that the *Palmella*-stages of *C. Franki* were favoured by concentrated solutions.

ductive phases and the cells of the colonies are held together solely by the mucilage in which they are embedded.

A remarkable form that is perhaps best dealt with here is *Physocytium*, an epiphyte on other freshwater Algae and seemingly only once recorded from Italy ((13) p. 71). One or more ovoid biflagellate cells exhibiting slight movements are enclosed within a globular mucilage-envelope attached to the substratum by two delicate threads (fig. 16 R, S). The swarmers sooner or later escape and, with intervening formation of *Palmella*-stages, become fixed to a new substratum by the tips of their flagella. If the latter really constitute the attaching mechanism this form is unique among Volvocales, and its inclusion in Chlamydomonadaceae is probably justified.

Returning to the ordinary *Palmella*-stages it may be noted that the individuals in this condition not uncommonly form hypnospores (thick-walled aplanospores) by contraction of the protoplasmic contents and their envelopment by a thick several-layered membrane (fig. 13 I); such hypnospores are frequently coloured red by haematochrome. Similar spores are sometimes produced from the contents of the ordinary vegetative cells after the flagella have been cast off. This is the customary method of tiding over a period of drought in *Sphaerella* (fig. 13 D) (165), and is also known in *Brachiomonas* (41) and in quite a number of species of *Chlamydomonas* (fig. 11 R), being especially typical for those responsible for red snow (*C. nivalis*, etc.) (120, 226). From such aplanospores in *Sphaerella*[1] extensive palmelloid stages can be produced by division of the cell-contents without the acquisition of flagella. Similar spores (often called cysts) are formed by a number of the Polyblepharidaceae (fig. 14 J). In *Coccomonas* (34), too, the individual, after withdrawal of the flagella, may thicken its wall and enter on a resting-stage, later liberating one or two swarmers (fig. 15 D, E).

THE COLONIAL FORMS

The numerous colonial members of the Chlamydomonadineae nearly all form colonies composed of a definite number of cells which is determined during early development, no cell-division occurring after the embryonic phase until a new reproductive phase sets in. Such definitely integrated colonies are spoken of as *coenobia*. It appears that the colonial habit has originated separately in Chlamydomonadaceae and in Sphaerellaceae and in both families has culminated in the development of a hollow sphere, beyond which further progress is impossible. In either case the simpler forms exhibit arrangement of the cells in one plane (*Gonium*, fig. 18 A; *Stephanosphaera*, fig. 13 E),

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[1] Freund (56) deals with the conditions under which swarmers are formed from these structures.

a production of coenobia from each cell of the parent, and an isogamous sexual process. Colonial forms also occur among the naked Polyblepharidaceae (*Raciborskiella*) and a doubtful colourless type (*Sycamina* (218)) is known. The only colonial form recorded from the sea is Zimmermann's *Oltmannsiella* ((236) p. 420).

In *Raciborskiella* (213, 230) (fig. 17 C) the more or less pear-shaped biflagellate cells are drawn out at their posterior ends, by means of which they are united to form a colony of 2–15 individuals which appear to possess the normal chlamydomonad structure. Multiplication of the cells takes place during movement and, according to Wislouch, it is not uncommon for the individual cells to become free, such cells by division forming new colonies.

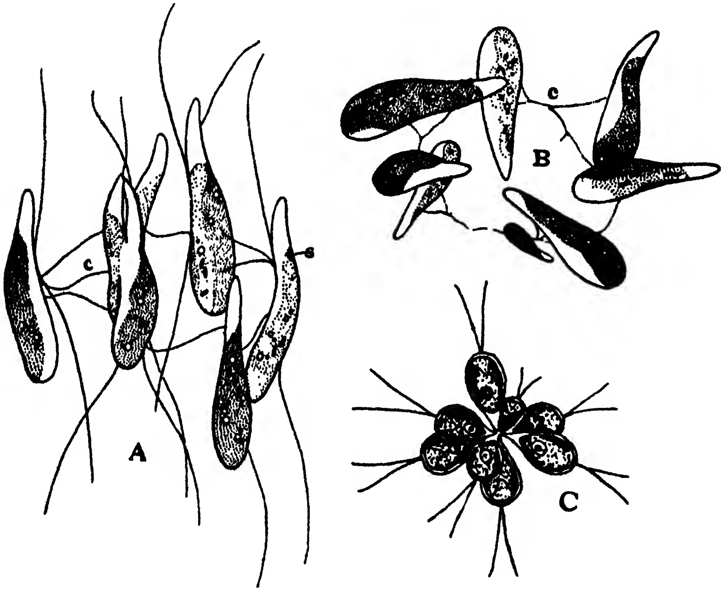

Fig. 17. Colony-formation among Polyblepharidaceae. A, B, *Dangeardinella saltatrix* Pascher (after Pascher). C, *Raciborskiella uroglenoides* Swirenko (after Swirenko). *c*, protoplasmic connecting strand; *s*, stigma.

Colonies of a rather more primitive type are also met with in Pascher's *Dangeardinella* (151). When cell-division occurs in this form, the daughter-individuals commonly remain joined by delicate simple or branched protoplasmic strands which may merely form a temporary connection or more usually persist. When such individuals divide again, colonies composed of four or more (up to 16) cells result, in which the connecting strands are often so delicate that they are only seen on careful examination (fig. 17 A, B, *c*). Whilst in some cases all the cells are grouped with their anterior ends pointing in one direction, more irregular groupings are the rule. *Dangeardinella* is the only dorsiventral form so far known to exhibit colony-formation, and the colonies are clearly of a less definite type than those of the majority of the Chlamydomonadineae. Neither here, nor in *Raciborskiella*, are they of the nature of coenobia.

Among the Chlamydomonadaceae both the di- and the tetrakontan series produce coenobia. The common *Gonium pectorale*[1] (fig. 18 A) has the form of a slightly curved plate with four central and 12 peripheral cells which possess chlamydomonad structure. The individual cells are connected by slight protrusions so that there are small triangular spaces between them, while in the centre of the whole coenobium there is a larger squarish area (*a*) occupied by mucus. The whole is embedded in mucilage (*m*) with a firm bounding layer (*b*). The peripheral cells are inclined at an angle to the axis of the plate (fig. 18 B), while the extremities bearing the flagella face towards the convex surface. During forward progression the whole plate spins round on its axis with the convex surface anterior. In cultures coenobia with eight or four cells or even the unicellular condition have been attained (82); such states are also found in nature.

In the other biflagellate forms the coenobia are oblong or spherical. Those of *Pandorina morum* (43, 169) (fig. 18 H) are composed usually of 16 (rarely 8 or 32) pyriform cells which are closely packed together with the broader ends outwards, a well-defined envelope of mucilage surrounding the whole. In *Eudorina*[2] (fig. 19 A) and *Pleodorina* (fig. 20 A) the coenobia are hollow, the cells forming a single layer in the peripheral mucilage, which is probably in large part composed of the gelatinous walls of the individual cells (fig. 19 C). The coenobia of *Eudorina*[3] are usually ellipsoidal and most commonly comprise 32 globose or somewhat pear-shaped cells grouped in well-marked transverse series, an anterior and a posterior tier of four and three intervening tiers of eight (cf. fig. 19 B, F). The two flagella of each cell pass out through one or two specially differentiated tubular canals (32, 71, 238) in the external mucilage of the colony (fig. 19 E). *Pleodorina* (20, 89, 127, 198) (fig. 20 A) has more numerous (128) cells which do not show the definite transverse arrangement met with in *Eudorina*. The cells of all these forms commonly contain a number of pyrenoids.

The coenobia of *Pandorina*, *Eudorina*, and *Pleodorina* exhibit a marked polarity, one end being always directed forwards during

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[1] See (10), (29), (78), (82), (131).

[2] A related form, *Volvulina* (68, 100, 160), has almost hemispherical cells directly apposed to the bounding membrane of the whole colony.

[3] See (32), (81), (89), (207).

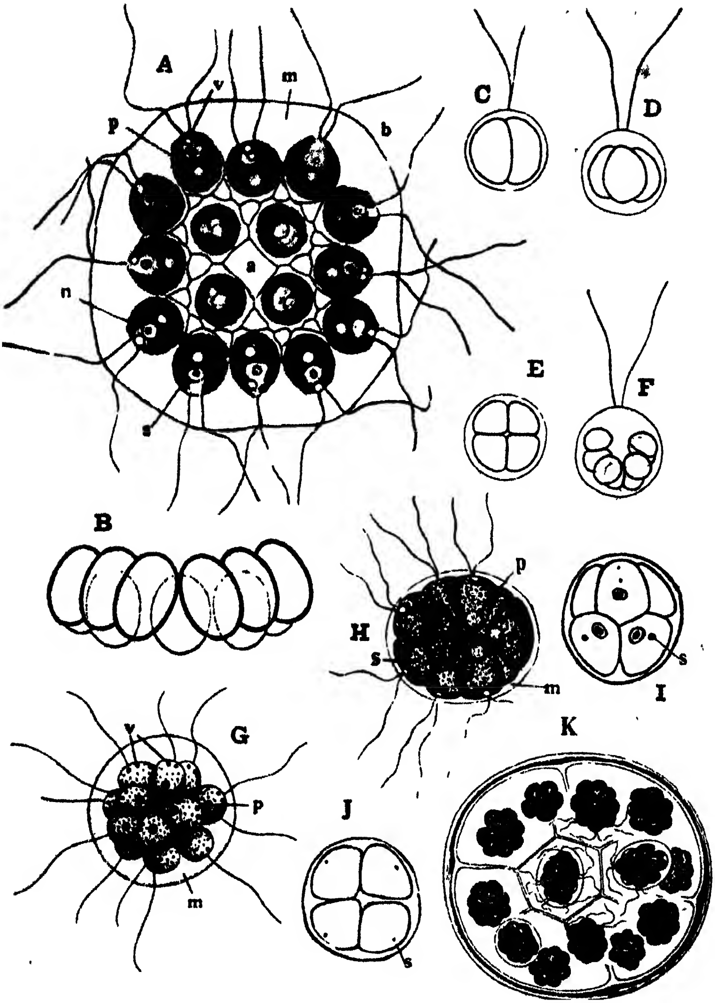

Fig. 18. A–F, *Gonium pectorale* Müll. (after Hartmann); B, side-view; C–F, stages in the development of a coenobium. G, *Mastigosphaera Gobii* Schew. (after Schewiakoff). H–K, *Pandorina morum* (Müll.) Bory (H and K after Pringsheim; I and J after Iyengar); I, coenobium from the anterior, and J, from the posterior end; K, coenobium undergoing asexual reproduction. *b*, bounding layer of mucilage; *a*, *m*, mucilage; *n*, nucleus; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole.

movement and, when the coenobia are ellipsoidal in form, the long axis of the ellipsoid is antero-posterior. The constituent cells show a definite orientation, the two flagella always lying in a plane at right angles to the antero-posterior plane of the whole coenobium, in which the two contractile vacuoles of the cell are situated. A further expression of the existing polarity is seen in the reduction (or occasional suppression?) of the eye-spots in the posterior cells (cf. fig. 18 J). The presence of protoplasmic connections (cf. fig. 19 C) between the cells has been established in most of these coenobic forms ((10) p. 345, (32), (78)), although in many cases they can only be detected with difficulty. As the coenobia mature and approach the phase of reproduction, such connections are withdrawn.

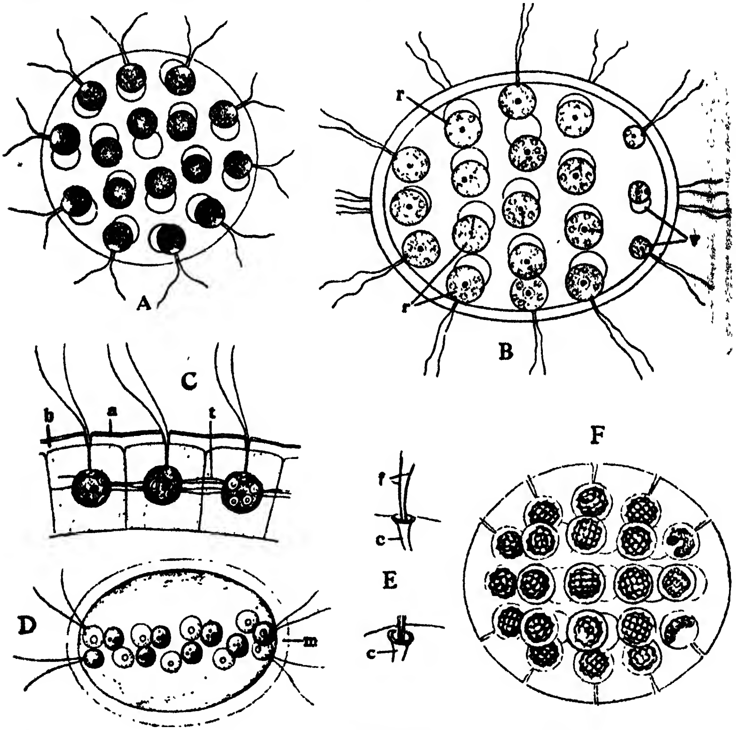

Fig. 19. A, C, E, F, *Eudorina elegans* Ehrenb.; A, vegetative colony; C, optical section showing protoplasmic connections (*t*); E, emergence of flagella; F, formation of daughter-coenobia. B, *E. illinoiensis* (Kof.) Pascher. D, *Stephanoon Askenasii* Schewiak. *a* and *b*, outer and inner layers of mucilage; *c*, collar around flagella; *f*, flagella; *m*, mucilage; *r*, reproductive, and *v*, vegetative cells. (A after West; B after Kofoid; C, E after Conrad; D after Schewiakoff; F after Hartmann.)

In *Gonium* and *Pandorina* (fig. 18 K) all the cells usually behave alike in reproduction, each cell of the coenobium for instance dividing to form a daughter-coenobium, although in the latter genus an occasional smaller anterior cell may fail to divide (36, 163); Crow (37) describes similar cases in *Gonium*. According to Hartmann ((81) p. 229) the four anterior cells in *Eudorina elegans* commonly divide less rapidly than the remainder, showing a certain lag with respect to the

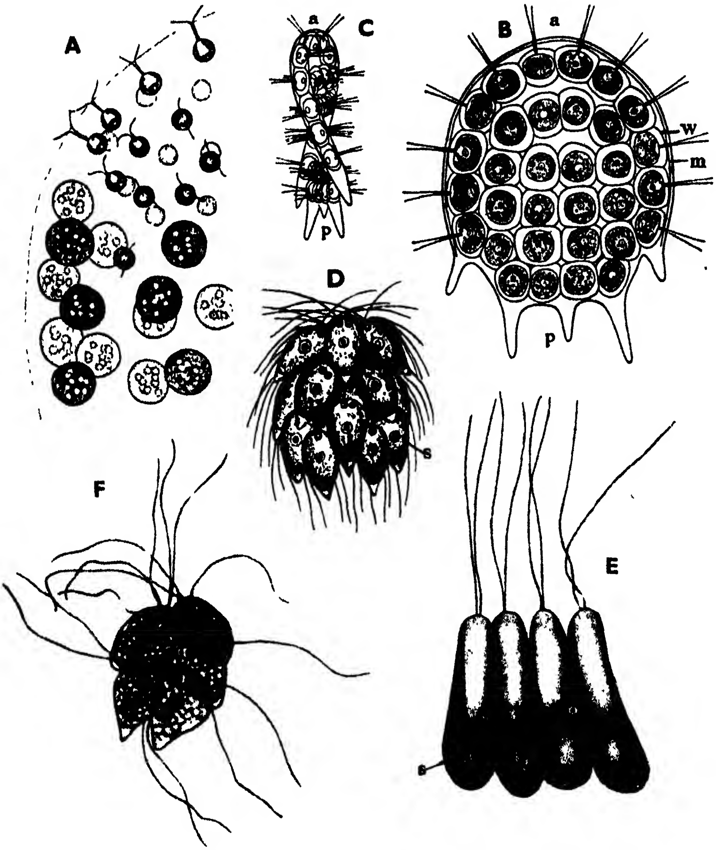

Fig. 20. A, *Pleodorina californica* Shaw, part of colony (after G. M. Smith). B, C, *Platydorina caudata* Kof. (after Kofoid); C, side-view. D, *Spondylomorum quaternarium* Stein (after Stein). E, *Oltmannsiella lineata* Zimmerm. (after Zimmermann). F, *Chlamydobotrys gracilis* Korschik. (after Schulze). *a*, anterior; *m*, mucilage; *p*, posterior; *s*, stigma; *w*, cell-wall.

others (cf. fig. 19 F), and these cells ordinarily play no part in the formation of sexual cells (cf. below). In *E. illinoiensis*[1] (fig. 19 B) these four cells remain much smaller and are either purely vegetative or divide later to form small 16-celled coenobia ((76) p. 174, (89)), while in the 64-celled *E. indica* (89) the cells of the front two tiers are smaller than the others. The increasing division of labour which can thus be traced reaches its culmination in this series in *Pleodorina californica* (fig. 20 A), where approximately half the cells of the anterior portion of the coenobium are smaller and purely vegetative. In another species (*P. indica* Iyengar (89)) vegetative cells are also scattered among the reproductive cells in the posterior half of the colony.

Only brief reference can be made to a number of less completely known forms. In *Stephanoon* (*Eudorinella*) ((57) p. 492, (182)) the spherical or ellipsoidal coenobia contain two transverse series of cells which alternate with one another (fig. 19 D). Schewiakoff's *Mastigosphaera* (182) shows great resemblance to *Pandorina*, except that the cells are uniflagellate (fig. 18 G). A more aberrant form is furnished by Kofoid's *Platydorina* (106, 207) which is at present only known from the United States ((208) p. 336). The coenobia (fig. 20 B) consist of a single layer of 32 cells, the enveloping mucilage (*m*) being rounded in front, but produced into three to five processes posteriorily. The coenobium is not, however, a flat plate, but as clearly seen in side view (fig. 20 C) has a marked spiral twist about the transverse plane; moreover, the flagella are borne alternately to the one side and the other. The cells are grouped in an outer series of 16, a median series of 12, and an inner group of four, and in the anterior half of the coenobium the cells of the successive series are separated by marked spaces. *Platydorina* could be derived from an *Eudorina* by imagining the coenobium of the latter compressed into one plane, and in this connection it may be mentioned that in *Eudorina* the mucilage-envelope is not uncommonly produced into mammillate processes at the posterior end. Nothing is known of the reproduction of *Platydorina*. The marine *Oltmannsiella* (236) is in so far remarkable that the four individuals lie in a row (fig. 20 E) and are naked until the time of reproduction.

In *Spondylomorum*[2] and *Chlamydobotrys*[3] (incl. *Chlamydosphaera* (187)) the coenobia are devoid of the common mucilage-envelope that is found in most of the previously discussed forms. The former[4] (fig. 20 D) has four, the latter (fig. 20 F) two flagella on the cells,

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[1] This is Kofoid's *Pleodorina illinoisensis* (105) which Pascher (147) has rightly referred to the genus *Eudorina* in view of the identical build of the colonies.

[2] See (209), (211), (212) p. 629.

[3] See (109), (146) p. 578, (193). Printz (170) places this under Playfair's *Uva* (160), but the latter is so imperfectly described and figured that it had better be ignored.

[4] Pascher ((147) p. 405) expresses doubts as to the existence of the quadriflagellate form (cf. also (193)). Schiller (185) has, however, described another species stated to have four flagella on the cells.

which in both cases are loosely arranged in tiers of four, the cells of successive tiers alternating with one another. The cells apparently rather easily separate. There is no pyrenoid in the chloroplast of either form. These two genera are marked saprobes and Jacobsen (91) first showed that *Spondylomorum* is readily obtained from cultivated soils. Korschikoff's *Pascheriella* (114) has four-celled coenobia with two cells only in each tier; the individual cells are very like those of some species of *Chlamydomonas*.

Among the Sphaerellaceae a coenobium of a relatively simple type is seen in *Stephanosphaera* ((31), (86), (193), (212) p. 626), where the spherical or ellipsoidal mucilage-envelope with a firm bounding layer contains usually eight (sometimes two, four or 16) cells arranged in the equatorial plane (fig. 13 E, p. 84). The protoplasts are elongate and provided with a number of simple or branched processes, developed especially at the two ends of the cells and extending up to the periphery of the mucilage. Whether a cell-membrane is present is doubtful (cf. (193) p. 519). The chloroplast is diffuse, parietal, and reticulate and commonly extends into the processes; often there are two pyrenoids, but there may be several. The contractile vacuoles are scattered over the whole protoplast. The anterior end bearing the two flagella is directed towards the outer surface of the whole coenobium, and the flagella penetrate the mucilage investment approximately in the equatorial plane.

The structure of the cells of *Stephanosphaera* thus shows considerable resemblances to those of a *Sphaerella* (p. 83), and this is also the case in *Volvox globator* and in certain other species of this genus. The coenobia of *Volvox*[1] are hollow spheres or ellipsoids with a single layer of very numerous (1500–20,000 in *V. globator*, 500–1000 in *V. aureus*) small cells occupying the periphery (fig. 21 A, B), while the interior is composed of diffluent mucilage. The whole coenobium is bounded by a delicate but sharply marked mucilage-lamella (fig. 21 E, *a*). In *V. globator* the middle lamellae of the cells form a polygonal pattern when the coenobium is viewed from the surface, while the protoplasts appear stellate with a number of coarse unbranched processes traversing the mucilaginous portion (*m*) of the membrane and corresponding with one another in adjacent cells (fig. 21 A, C). The processes on the two sides of the middle lamella are connected with one another by delicate plasmodesmae (129) traversing the latter (fig. 21 D).[2] In optical section the protoplast is seen to occupy only a small part of the cell-cavity, being markedly compressed with the processes developed only in a plane parallel with

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[1] See (30), (79), (89), (94), (102), (103), (128), (129), (138), (161–164), (179).

[2] Many writers erroneously speak of the processes as protoplasmic connections, but the latter are not in any way comparable to the delicate connections found in the other colonial Volvocales and seen also in *Volvox*.

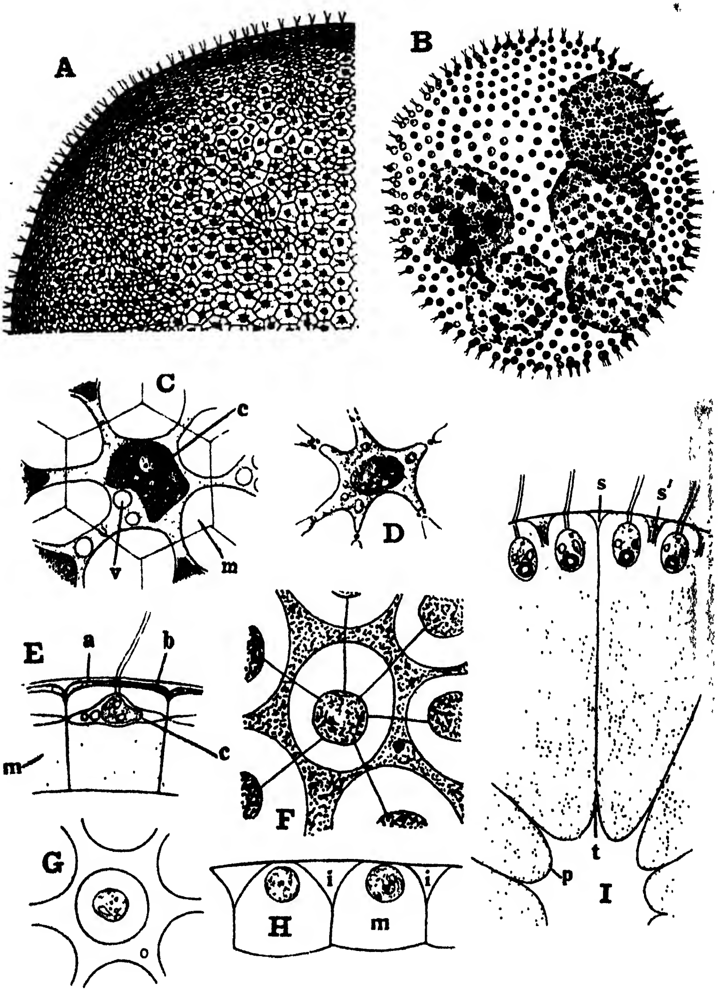

Fig. 21. A, C–E, *Volvox globator* (L.) Ehrenb.; A, part of coenobium; C, D, cells in surface-view, D after removal of the middle lamella; E, section of periphery of coenobium. B, *V. Mononae* Smith, with daughter-coenobia. F, I, *V. aureus* Ehrenb.; F, from the surface (diagrammatic); I, section of part of coenobium. G, H, *V. tertius* Meyer; G from the surface, H in section. *a*, boundary of mucilage-envelope; *b*, external cell-wall; *c*, chloroplast; *i*, intercellular space; *m*, mucilage of wall; *p*, inner boundary of mucilage-prism; *s*, outer part of septum; *t*, lateral boundary of same; *v*, contractile vacuole. (A, B after G. M. Smith; C–F, I after Meyer; G, H after Pascher.)

the contour of the coenobium (fig. 21 E). An entire cell has the form of a five- or six-sided prism (cf. fig. 21 C, E) tapering very slightly towards the interior of the coenobium from which it is demarcated by a flat wall. The chloroplast (*c*) is a curved plate with one or more pyrenoids and usually extends into the basal portions of the processes. A number (2–6) of contractile vacuoles (*v*) are scattered through the protoplast.

In *V. aureus* a surface-view of the coenobium presents a similar appearance to that seen in *V. globator*, but the protoplasts appear rounded and their processes, which again all lie in one plane, are delicate and usually only two or three per cell (fig. 21 F). As a general rule they are not apparent without staining. In optical section the appearance is altogether different from that of the other species. The protoplasts are oblong and occupy the periphery of wedge-shaped mucilage-prisms that extend radially almost to the centre of the colony (fig. 21 I). The details are not altogether clear, but to judge from Meyer's figures (129) the prisms probably represent the contours of the actual cells which are here produced inwards almost to the centre of the coenobium (cf. (147) p. 452). It would seem that not every individual cell occupies such a prism, but that each of the latter harbours a number of protoplasts which are separated only by short strips of membrane (*s*′) extending a little way inwards from the periphery (fig. 21 I). The cells of *V. aureus* possess to all intents and purposes a chlamydomonad structure, the chloroplast not extending into the protoplasmic processes.

In the case of *V. tertius* (129) the protoplasts are globose and, except in the young coenobia(?), devoid of protoplasmic connections (fig. 21 G).[1] The optical section of the cells (fig. 21 H), apart from the circular form of the protoplasts, is similar to that of *V. globator*. The outer walls, however, are rounded, so as to leave prominent intercellular spaces (*i*) between them, and in the surface view one sees a network of cell-membranes with the protoplasts located in the rounded meshes (fig. 21 G). The details of the cell-structure are not known. G. M. Smith (206) has further described a species, *V. Mononae* (fig. 21 B), which has also been found in Great Britain, in which the protoplasts have altogether the chlamydomonad structure and in which protoplasmic processes are apparently lacking at all stages of the life-history.[2]

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[1] Cf. also *V. africanus* (89, 161) and *V. gigas* (161).

[2] According to Zimmermann ((235) p. 402, footnote) *Volvox globator* in alkaline solutions loses its protoplasmic processes and then altogether resembles Shaw's genus *Merrillosphaera* (202). Mr D. J. Scourfield, however, informs me that he has found a form, similar to *Volvox Mononae* and devoid of protoplasmic connections, in the same pool together with *V. globator* and *V. aureus*.

Apart from these four species a number of others have been studied, in part in great detail (cf. (89), (161–164), (179), (200–204)), and it is evident that there exist in other parts of the world certain variants of these principal types. The detailed studies undertaken by Shaw, Pocock, and Iyengar, however, in most cases leave it unclear whether these variants deserve a specific status and are not perhaps merely regional modifications of the known European species. It seems undoubted that in the present genus *Volvox* forms with rather diverse types of cell-structure are included. The type of *V. globator* with its coarse processes, diffuse chloroplast, and scattered contractile vacuoles shows great similarity to the *Sphaerella*-type (36). In *Volvox aureus*, on the other hand, quite apart from the peculiar build of the coenobium as a whole, the protoplast appears to have a rather different structure. The processes are quite subsidiary to the main protoplast which in essentials is that of a *Chlamydomonas*, and this is still more true of *Volvox Mononae.* It may well be that, as our knowledge of the species of *Volvox* increases, it will become necessary to segregate the genus into a number of genera, some belonging to the Sphaerellaceae, others (*V. aureus*, *V. Mononae*) to the Chlamydomonadaceae. *V. Mononae* may well be a further advance on *Pleodorina.*

Such a segregation of *Volvox* into a number of genera has been advocated by Shaw, but on rather a different basis, viz. mainly on the degree of development of the daughter-colonies at the time of liberation. In all the species of *Volvox* the daughter-colonies arise from specially enlarged cells, so-called *gonidia*, which are produced usually in small numbers in the posterior half of the colony. They are recognisable at an earlier or later stage in development by their larger size, their larger nuclei, and the possession of more numerous protoplasmic processes (fig. 22 A) which are here only withdrawn at a late stage. In Shaw's *Besseyosphaera* (199) the gonidia are only formed after liberation of the daughter-coenobia from the parent. In *Copelandosphaera* (203) gonidia are developed, but do not commence to divide until the coenobium is set free, while in *Merrillosphaera* (202, 204) the gonidia have already developed to a varying extent into daughter-coenobia when the parent is liberated. According to Shaw these two genera lack protoplasmic connections between the cells.[1] *Volvox aureus*, owing to the peculiar structure of the coenobium, is placed by Shaw in a separate genus, *Janetosphaera* (201). This treatment of the species of *Volvox* has been criticised by Pascher ((147) p. 463) on the ground that the time of development of the gonidia into daughter-coenobia no doubt depends in part on external conditions. In any case the validity of Shaw's genera cannot be estimated until the details of cell-structure are known for the various forms involved.

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[1] Cf. footnote 2 on the previous page. Iyengar ((89) p. 357) has shown that protoplasmic processes are present in *Copelandosphaera.*

Asexual Reproduction of the Colonial Forms

As already mentioned, in all the colonial Chlamydomonadineae, except *Raciborskiella* and *Dangeardinella*, the individuals producing daughter-coenobia undergo division within their membrane to form the full complement of cells of the future coenobium and, after the latter's liberation, there is no further cell-division until a new reproductive phase sets in. In *Pleodorina* only about half, and in *Volvox* only a few, of the cells (*gonidia*) divide in this way. All the divisions, as in the unicellular types, are longitudinal[1] and, although this has only been fully established in the commoner forms, in general they follow a definite sequence (78, 82, 102, 103, 118, 127, 162, 235)[2] (fig. 22). The first division plane seems always to coincide with the antero-posterior plane of the whole coenobium, i.e. it is longitudinal with respect to the parent-coenobium as a whole (fig. 22 C, D). The second division is longitudinal in a plane at right angles to the first (fig. 18 D, E) and, after that, each of the four resulting cells divides again lengthwise so that an eight-celled plate (plakea-stage), which has become more or less incurved with the concave surface outwards, is produced (fig. 18 F). At this stage the position of the cells becomes adjusted, so that four form a central group, while four are peripheral, each lying opposite the line of separation between two cells of the central group. Further longitudinal divisions (fig. 22 F) leading to the establishment of the definitive number of cells are accompanied by an increasing curvature of the plate till, in all except *Gonium*, the cells ultimately form a hollow sphere with a small aperture towards the exterior of the parent-coenobium (figs. 19 F, 22 G, 23 A). At this stage the cells are still naked and all are naturally so orientated that the anterior end of the cell is directed towards the concave side of the plate or towards the centre of the sphere. Under abnormal conditions the plakea-stage may be retained in *Eudorina* (82).

The normal orientation is attained by a complete inversion of the young coenobium, first demonstrated by Powers[3] ((164) p. 158) in two species of *Volvox* in 1908 and since shown to occur also in the other common members (cf. (82), (118), (203), (235)); a very detailed

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[1] Schiller ((185) p. 278), however, states that the second division plane is transverse in the development of the daughter-coenobia of *Spondylomorum caudatum*.

[2] Exceptions are found in *Oltmannsiella* where, after the protoplast has divided longitudinally, there is a rotation to the transverse plane, followed by a second longitudinal division in a plane parallel to the first (236), and *Chlamydobotrys* ((193) p. 560) where the protoplast divides by successive fission to form the new colony without the development of a plate-stage.

[3] In describing the development of the daughter-colonies in *Eudorina illinoiensis* Merton ((127) p. 470) recognised that inversion occurred without establishing the manner in which it was accomplished.

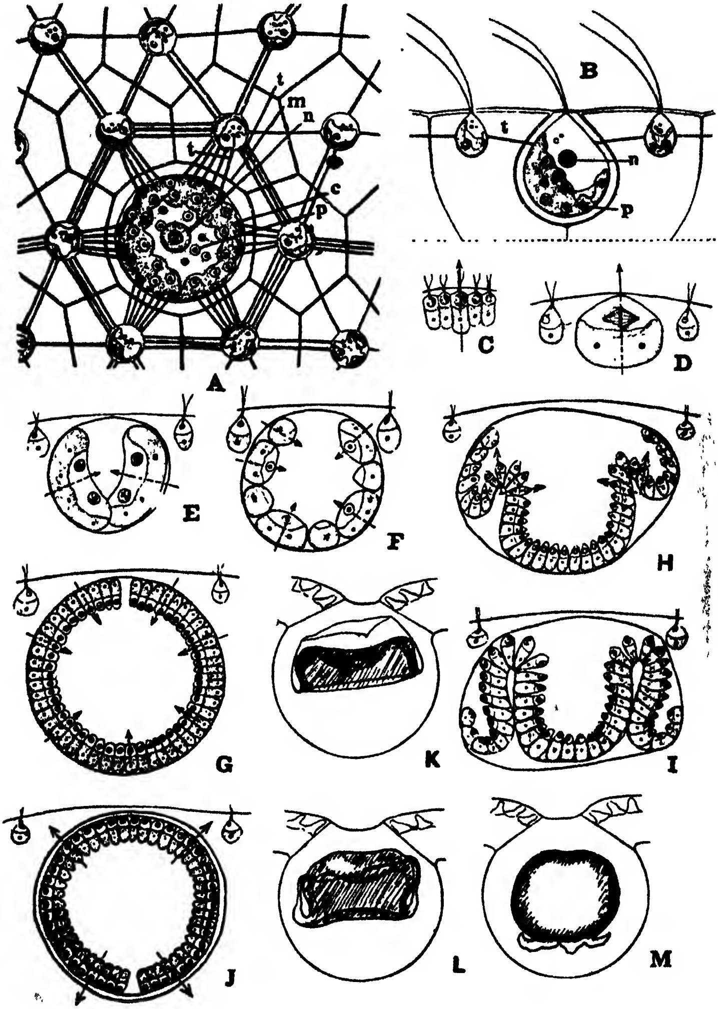

Fig. 22. A–J, Colony-formation in *Volvox aureus*; A, part of a coenobium with a gonidium in surface-view; B, section with an enlarging cell (gonidium or oogonium); C, gonidium just commencing to enlarge; D, the same later, first nuclear division; E, two-celled stage; F, later stage, incurving; G, final stage of young embryo; H, I, two stages in inversion; J, inversion completed. K–M, *Volvox* sp., three stages in inversion. *c*, chloroplast; *m*, cell-wall; *n*, nucleus; *p*, pyrenoid; *t*, protoplasmic processes. (A, B after Janet; K–M after Pocock; the rest after Zimmermann.)

description is given by Pocock (162). This process commences with a slight constriction in the equatorial region of the sphere, after which the part opposite to the aperture (i.e. the surface adjacent to the interior of the parent-coenobium) begins to fold into the anterior half (fig. 22 K). As this invagination progresses the aperture greatly enlarges and, as the infolding posterior portion begins to push through it (fig. 22 L), its edges curl backwards and gradually slide down (fig. 22 I) until the whole structure is inverted. The anterior ends of the cells now face outwards (fig. 22 J). The aperture at this stage shows a number of lobes (fig. 22 M) which gradually fold in to close it.

During these happenings the hitherto naked protoplasts often acquire cell-membranes, although this is apparently delayed in some forms till after the liberation of the new coenobium. In the species of *Volvox* the daughter-colonies are set free into the interior of the parent-colony (figs. 21 B, 23 B) which may continue to live and move for some time, but sooner or later the parent tears open irregularly and almost immediately dies, while the daughters start an independent existence. In all the forms just considered the aperture on one side of the sphere, which not uncommonly fails to close completely, comes to lie at the anterior pole of the new coenobium. Under abnormal conditions the inversion may fail to occur (cf. (219)).

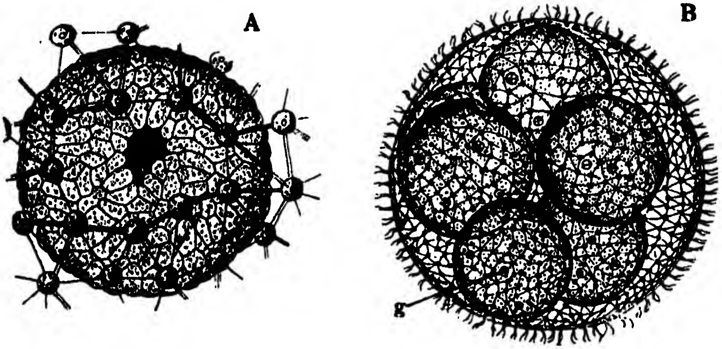

Fig. 23. *Volvox aureus* (after Klein). A, young coenobium seen through part of surface of parent, showing the aperture in the sphere. B, colony with daughter-individuals in which dividing gonidia (*g*) are already recognisable.

In *Volvox* a large part of the parent-coenobium perishes after reproduction, and this is also true of *Pleodorina* and, to a more limited extent, of *Eudorina illinoiensis*. This is in marked contrast to all the unicellular forms and the less specialised coenobial types in which the entire living substance of the parent is perpetuated in the offspring.

The division of labour in these more advanced types thus brings with it the death of the vegetative part (soma) of the colony. These considerations indicate too the difficulty of drawing a sharp line between colony and individual in the Volvocales. Forms with specialised reproductive cells, although one may speak of them as colonies with division of labour, in fact behave as individuals, and the presence of protoplasmic connections in most of the coenobial Chlamydomonadineae renders the individuality of the colony the more marked.

Occasional liberation of individual cells may, however, occur ((147) p. 77) and Bock (10) showed that single cells or groups of cells artificially detached from the coenobia of *Gonium*, *Pandorina*, and *Eudorina* survive, although as a general rule they soon proceed to divide to form new colonies; so far such experiments have been unsuccessful with *Volvox*. It is of interest that, while detached cells of *Gonium* give rise to new colonies of normal size, those of *Pandorina* are smaller than usual, whilst in *Eudorina* the total number of individual cells is reduced. The progressive specialisation seen in other features thus also shows itself here. According to Schreiber ((191) p. 343), when colonies of *Gonium* and *Eudorina* are subjected to progressive desiccation, they pass over into a palmelloid condition in which the two genera become practically indistinguishable; on transference to water the cells are liberated as single swarmers which, sometimes only after two or three days, divide to form normal coenobia (cf. also (24), (47)).

SEXUAL REPRODUCTION OF THE CHLAMYDOMONADINEAE

A large proportion of the forms above discussed readily resort to sexual reproduction, and in this respect, if in no other, the Chlamydomonadineae show a higher status than do the flagellate series of other groups of Algae. Even the naked Polyblepharidaceae, once regarded as devoid of the capacity for sexual reproduction, are now known to possess it. In the case of *Dunaliella* (217) and *Polytomella* (3) the process consists in the fusion of two ordinary individuals (*hologamy*, fig. 24 A, B),[1] with the production of a motile zygote which in the case of *Dunaliella* bears only two flagella, those of one gamete being apparently shed during the process of fusion. In *Phyllocardium* (113) (fig. 24 C–E) the small gametes, which unlike the vegetative individuals are not compressed, are formed by repeated division. The gametes of *Dangeardinella* (151), lastly, vary greatly in size, but both gametes of the same size (fig. 24 G), as well as others of very unequal dimensions (fig. 24 H), are found to fuse (cf. below).

In the remaining isogamous members of the Chlamydomonadineae

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[1] Korschikoff (110) produces some evidence for the occurrence of a similar sexual process in *Pyramimonas*. According to Pascher ((147) p. 92) conjugation may occur in this genus between the cells of *Palmella*-stages.

(40, 49, 73, 175) the gametes are formed by division of the contents of the ordinary cells after the manner above described for vegetative division, fission into 16 or even into 32 or 64 (e.g. *Sphaerella*, fig. 25 A) parts being not uncommon; in *Sphaerella lacustris*, however, the gametes appear always to be formed from cells which have entered upon a resting period ((157), (193) p. 539). The gametes are set free as small, usually naked swarmers which otherwise as a rule resemble the vegetative individuals in all essentials (fig. 25 B). In some species of *Chlamydomonas* (e.g. *C. media* Klebs (101)) and *Chlorogonium* ((193) p. 529, (212) pp. 627, 644), as well as in *Lobomonas* (85) and *Diplostauron* (110), the gametes are provided with a membrane which is often discarded before fusion (fig. 25 E, F).

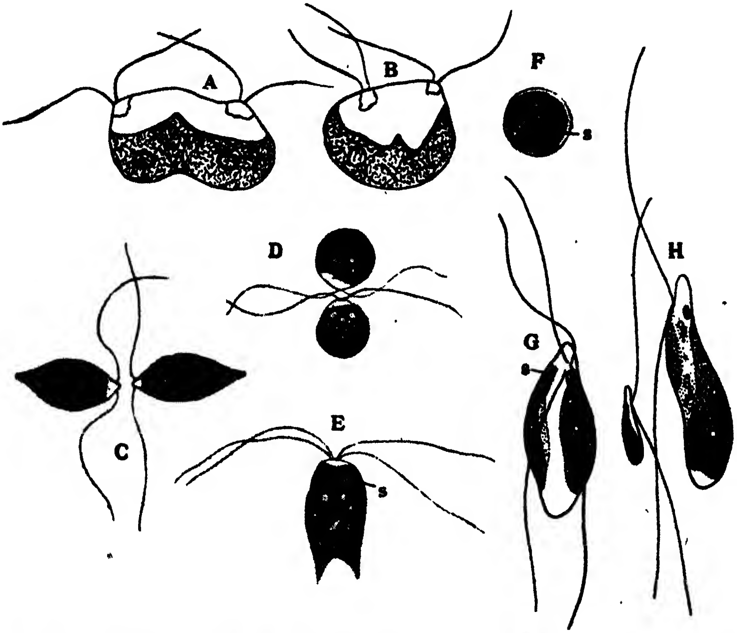

Fig. 24. Sexual reproduction of the Polyblepharidaceae. A, B, *Dunaliella salina* Teod. (after Teodoresco). C–F, *Phyllocardium complanatum* Korschik. (after Korschikoff); E, zygote; F, zygospore. G, H, *Dangeardinella saltatrix* Pascher (after Pascher); G, zygote resulting from equal fusion; H, unequal gametes. *s*, stigma.

Various observers (see (212) p. 671) have recorded the secretion of a hyaline substance at the bases of the flagella by means of which the two gametes become cemented together (fig. 25 I). In most cases fusion occurs only between gametes from different parent-individuals. In the formation of the zygote the two gametes are usually equally concerned (fig. 25 C, E), but in *Chlamydomonas monoica* (212), where the gametes are provided with membranes, the contents of one pass over entirely into that of the other (fig. 25 J); this is also sometimes the case in *C. eugametos* (133) (fig. 111 G, p. 352). Gametes which fail to fuse may sometimes develop into normal vegetative individuals. There are probably all gradations in this respect between forms like *C. eugametos*, in which according to Moewus (133) every individual can act as a gamete providing the conditions for sexual fusion are realised, and forms with specialised gametes which are incapable of independent further development (e.g. *Stephanosphaera*). Clump-formation has been recorded by Pascher (152) and Moewus.

Pascher (145) has observed amoeboid gametes devoid of flagella in an undetermined species of *Chlamydomonas* (fig. 25 H). The likewise amoeboid zygotes fuse with one another, as well as with other amoeboid gametes, forming plasmodia which ultimately encyst. At present no other case of this kind has been recorded.

The ordinary gametes of the unicellular forms not uncommonly vary appreciably in size, a feature also clearly seen in *Pandorina* (fig. 26 B) and, when large and small gametes fuse together, an impression of marked anisogamy[1] is afforded; but in most species showing this phenomenon numerous fusions between two large or two small gametes are likewise observed.[2] In other words such forms fluctuate between isogamy and anisogamy, and only in *Chlamydomonas Braunii*, *C. coccifera*, *Phyllomonas striata*, and *Chlorogonium oogamum*, as well as in the oogamous coenobial types, has, as far as our present knowledge goes, the anisogamy become fixed.

In the case of *Chlamydomonas Braunii* (72) the macrogametes are formed in fours and, apart from slight differences in shape, resemble the parent-cells, although always larger than young vegetative individuals. The microgametes, formed to the number of eight from their mother-cells, are about half the size of the others, smaller than the young vegetative individuals, and relatively more elongate. According to Goroschankin the large gametes soon come to rest without drawing in their flagella and are sought out by the microgametes which show active movement (fig. 25 K). Both are clothed in a cell-wall. In fusion (fig. 25 K–M) the gametes become joined by their anterior extremities, where the membranes coalesce, and the contents of the smaller drift over into those of the larger, so that the fused protoplasts are surrounded in the first place by a wide envelope

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[1] In *Chlamydomonas eugametos*, where such features are also seen, Moewus (133) states that the contents of the smaller always pass over into those of the larger gamete, although the smaller may belong to either strain (cf. p. 43). The difference of size is therefore in this case not a sexual difference.

[2] See (26), (89), (108), (147) p. 60, (153) p. 474, (169).

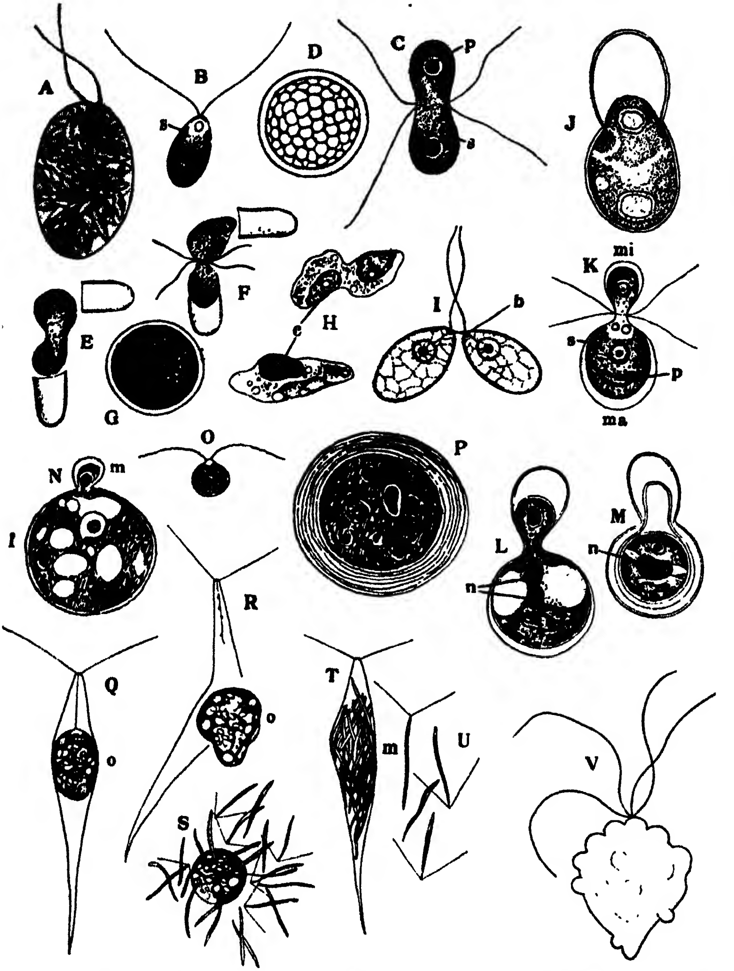

Fig. 25. Sexual reproduction of unicellular Chlamydomonadineae. A, *Sphaerella droebakensis* (Wollenweb.), gamete-formation. B–D, *Chlamydomonas Reinhardi* Dang.; B, gamete; C, fusion; D, zygospore. E–G, *C. media* Klebs; G, zygospore. H, *Chlamydomonas* sp., above fusion of amoeboid gametes, below amoeboid zygote. I, *Polytoma uvella* Ehrenb., junction of gametes. J, *Chlamydomonas monoica* Strehlow, anisogamous fusion. K–M, *C. Braunii* Gorosch., three stages in sexual fusion. N–P, *C. coccifera* Gorosch.; O, microgamete; N, fusion; P, zygospore. Q–U, *Chlorogonium oogamum* Pascher; Q, formation and R, liberation of ovum; T, formation of male cells (U); S, fertilisation. V, *Chlamydomonas botryodes* Strehlow, zygote. *b*, basal granule; *c*, chloroplast; *f*, female; *m*, male; *ma*, macro-, and *mi*, microgamete; *n*, nucleus; *o*, ovum; *p*, pyrenoid; *s*, stigma. (A after Wollenweber; E–G after Klebs; H, Q–U after Pascher; I, J, V after Strehlow; the rest after Goroschankin.)

formed by the combined membranes of the gametes. During the process of fusion the flagella disappear. Later the zygote secretes its own close-fitting membranes in the usual way. In *Phyllomonas* (111) matters are much the same, but there is a more pronounced difference in size between the two kinds of gametes, while the microgametes are naked.

Chlorogonium oogamum (153) produces a single ovum from the contents of the elongate vegetative individual (fig. 25 Q) and the ovum is set free as a naked amoeboid protoplast, devoid of flagella, through a lateral rupture in the wall of the parent (fig. 25 R). The narrow elongate spermatozoids are formed in large numbers by rapid successive division of the contents of an individual (fig. 25 T); their chloroplast is yellowish green and they possess a delicate membrane and a pair of apical flagella (fig. 25 U). The oospore at first secretes a delicate membrane within which the definitive oospore-membranes are formed (cf. *Sphaeroplea*, p. 224).

The macrogamete of *Chlamydomonas coccifera* (74) is formed from the ordinary vegetative individual without division. The flagella are lost and a considerable enlargement and rounding off takes place, accompanied by increase in size of the pyrenoids (cf. fig. 25 N, *f*). The male gametes (fig. 25 O), formed by the division of the parent-cells into sixteen parts, are nearly spherical, the flagella are markedly longer than the body, and there is usually but a single pyrenoid. Both gametes are again clothed in a cell-wall. The male gamete unites with the female at the point where the anterior papilla of the latter was situated (fig. 25 N). The sexual differentiation of the two species last discussed almost amounts to oogamy, although the male swarmers are not the typical spermatozoids, found in the coenobial forms to be considered below. *Chlorogonium oogamum* is the more primitive of the two in the fact that the ovum is set free from the female cell.

Among the coenobial members of the Chlamydomonadineae an essentially isogamous sexual process has been observed in *Raciborskiella* (230) (hologamy, p. 109), *Gonium*, *Pandorina*, *Chlamydobotrys* ((212) p. 658), and *Stephanosphaera*. In the last-named (86, 133) the gametes are long spindle-shaped bodies with a pointed posterior end and a pair of rather short flagella (fig. 13 F, p. 84) and are formed by division of usually all the cells of a coenobium into 4–32 parts (fig. 13 K). As in many of the unicellular types the zygote (fig. 13 G) remains motile for some time before rounding off to form the resting zygospore (fig. 13 H, J). Both *Gonium* ((108), (191) p. 353) and *Pandorina* (169) show the fluctuating anisogamy above described for certain Chlamydomonadaceae, but in *Pandorina* there appears to be a greater tendency for gametes of unequal size to fuse together than in *Gonium* and the unicellular forms. The former genus thus shows perhaps a trend in the direction of the establishment of a more definite anisogamy, such as has culminated in the pronounced oogamy of *Eudorina*, *Pleodorina* and *Volvox*. Both in *Gonium* (108, 194) and *Pandorina* (fig. 26 A) the sexual coenobia are of small dimensions and the gametes are constituted by the naked protoplasts which escape from the membranes.

Eudorina ((69) p. 41, (71)) and *Pleodorina* are dioecious, although the coenobia of the former occasionally include both sexes ((18), (147) p. 62); the male coenobia of *Pleodorina* are smaller than the female

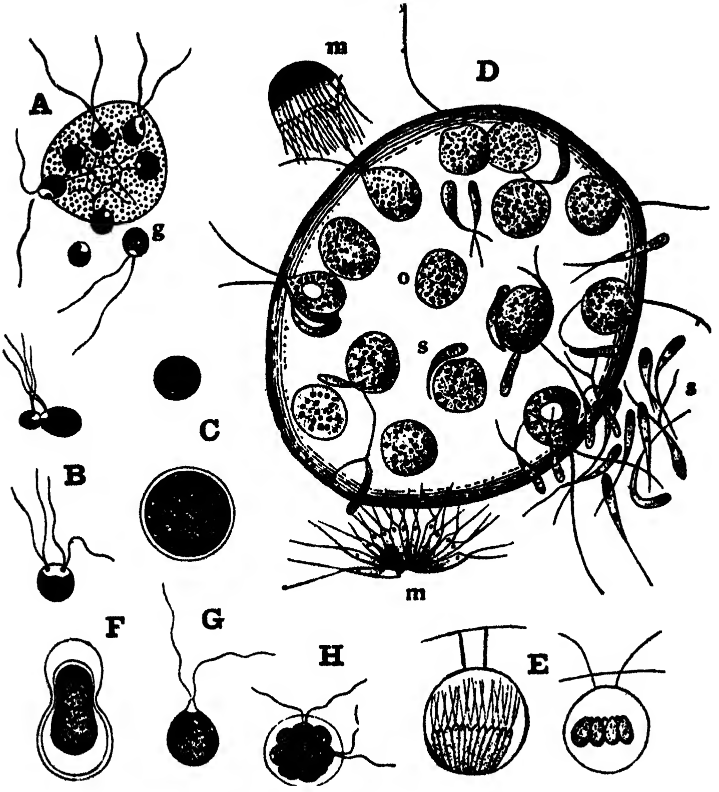

Fig. 26. Sexual reproduction of *Pandorina* and *Eudorina*. A–C, F–H, *Pandorina morum* (after Pringsheim); A, sexual coenobium showing liberation of gametes (*g*); B, unequal and equal fusion; C, young and old zygotes; F, germination of zygospore; G, swarmer liberated from same; H, new coenobium formed from the latter. D, E, *Eudorina elegans* (after Goebel); D, female coenobium with ova (*o*) surrounded by spermatozoids, in part still in bundles (*m*), in part free (*s*); E, two stages in the formation of spermatozoids, the earlier on the right.

and pale yellowish in colour (20). The female coenobia of *Eudorina* altogether resemble the vegetative colonies, i.e. the ordinary cells (as in *Chlamydomonas coccifera*) develop into ova with some enlargement, but without division (fig. 26 D). In *E. illinoiensis* (76, 89, 127) the four anterior cells usually remain sterile and this is possibly true of all the species of the genus. In the male coenobia these cells only very rarely appear to take part in the formation of antheridia. The spermatozoid-bundles of the latter are formed by successive division following the same sequence as in ordinary vegetative multiplication, but usually culminating in the production of 64 units and unaccompanied by any appreciable incurling of the resulting plate (fig. 26 E). The individual spermatozoids are elongate with a pointed anterior extremity and the chromatophore becomes yellowish. The male platelets are liberated intact and swarm to the female colonies where they undergo disintegration into the individual sperms (fig. 26 D, *m*, *s*). At this stage the membranes of the ova (*o*) have gelatinised (71, 89). In *Pleodorina californica* (20) ova and antheridia are formed only from the cells of the posterior half of the coenobium; as in asexual reproduction, therefore, the cells of the anterior half are purely vegetative. The sexual cells develop in the same way as in *Eudorina*.

Among the species of *Volvox* (30, 102, 103, 162, 233), some like *V. aureus* are commonly dioecious, others like *V. globator* are monoecious, but colonies of *V. aureus* with both ova and antheridia are not infrequent; according to Mainx (126) such differences are probably distinctive of physiological races. Sexual coenobia are frequently devoid of gonidia, but this is not always the case. Monoecious coenobia are often markedly protandrous, although those of *V. aureus* are mostly protogynous. Both kinds of sexual elements are developed only in the posterior half of the coenobia and usually in small numbers; they are often recognisable in early stages by increased size, and in later stages the ova are distinguishable from the gonidia by the absence of division. The female cells ultimately appear as greatly enlarged flask-shaped cells (fig. 27 A, B). Their protoplasts protrude markedly into the interior of the coenobium and are surrounded by a relatively firm and close-fitting membrane (cf. fig. 22 B). At maturity they bear no flagella. These cells might well be described as oogonia, since it is their protoplast alone that functions as the female gamete, while the beak-like apex of the membrane, by means of which these cells communicate with the surface of the coenobium, probably marks the point of entry of the male gamete.

In the antheridial cells numerous spermatozoids are produced by successive division following the same plan as in vegetative segmentation; they remain grouped as a flat plate (fig. 27 B) or, in some species (occasionally in *V. aureus*), become inrolled to form a sphere which becomes inverted just like the vegetative coenobium (162). The spermatozoids are very narrow elongate structures with a small yellow-green or pale green chromatophore and a long pointed anterior extremity bearing the two flagella, either apically or subapically (fig. 27 C). The actual process of fertilisation has not yet been observed in *Eudorina* and *Pleodorina*, while the data for *Volvox* (122) are not very convincing. The oospores of *Volvox* are commonly spiny (fig. 27 E) and remain in the parent-coenobium for some little time after fertilisation. Parthenospores have been recorded by Mainx (126) in *Volvox aureus* and *Eudorina elegans*.

There appears to be a great uniformity in the sexual reproduction of *Volvox*, a fact which, if confirmed, would perhaps rather speak against a polyphyletic origin of the genus (cf. p. 105). The oogamy is here clearly of a more specialised type than that of *Eudorina* or *Pleodorina*.

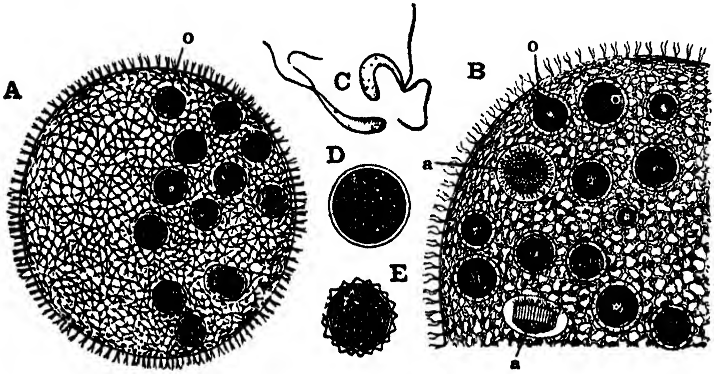

Fig. 27. Sexual reproduction of *Volvox*. A, C, D, *V. aureus*; A, female colony with oogonia (*o*); C, spermatozoids; D, oospore. B, E, *V. globator*; B, part of a monoecious coenobium with oogonia (*o*) and antheridia (*a*); E, oospore. (A, C after Klein; B, after Cohn; D, E after West.)

THE FURTHER DEVELOPMENT OF THE ZYGOTE

Nuclear fusion does not necessarily occur immediately after fusion of the protoplasts, while fusion of the nucleoli is stated to ensue some time after the nuclei have amalgamated (cf. (212) p. 665). Especially among the unicellular forms there are all transitions between cases in which the gametes come to rest just prior to fusion and those in which the zygote retains its flagella and continues to move for a shorter or longer period before coming to rest. Sooner or later, however, the product of sexual fusion (often after considerable enlargement) becomes enveloped in a thick usually stratified membrane,[1] partly consisting of cellulose ((193) p. 523), while the green colour of the contents mostly becomes obscured by the accumulation of large quantities of an oil coloured red or orange; the coloration is probably due to haematochrome. Such zygotes can pass through a prolonged resting period, and it is probable that a certain interval must normally elapse before germination can take place.

There can be little doubt that reduction always occurs during the germination of the zygotes, although the actual cytological details appear to have been observed only in *Volvox* (233) and *Stephanosphaera* ((133) p. 512). The fact, however, that in all cases that have been carefully studied, two divisions have been found to occur during the germination of the zygote speaks clearly for the occurrence of a reduction division.

The production of four (rarely eight) swarmers has been recorded for species of *Chlamydomonas* (e.g. *C. Ehrenbergii*, fig. 28 G–K; cf. also (175)) and other unicellular forms ((193), (212) p. 686) (fig. 28 B, C), as well as for *Stephanosphaera* (cf. (212) p. 678) and *Gonium* ((191) p. 356, (194)). In *Stephanosphaera* (fig. 28 A) the swarmers remain distinct and each forms a new coenobium, whilst in *Gonium* they remain united to form a small 4-celled plate (fig. 28 F), from each of whose cells a normal 16-celled coenobium is soon formed. In *Pandorina* (108, 169) and *Eudorina* ((137), (191) p. 363) (fig. 28 E), however, only one of the four resulting cells normally survives, although remains of the other three[2] are to be found within the enlarged zygote membrane before the single successful swarmer, which commonly retains some of the red-coloured oil of the zygote, escapes. This swarmer soon divides to form a normal coenobium. Pascher ((147) p. 65) expresses the opinion that some of the unicellular forms may behave like *Eudorina*.

In *Volvox* (162) the contents of the oospore, after liberation (fig. 28 L), may give rise to a single swarmer (fig. 28 M). The protoplast of the latter divides to form a hollow sphere of cells (fig. 28 N, O) which, after the usual inversion (fig. 28 P, Q), is set free as a few-celled coenobium, those of the mature size being formed only after a number of generations. Pocock refers to the possibility of several swarmers being formed, of which perhaps only one is successful, while according to the older account of Kirchner (99) the new coenobium may be produced by division of the motionless contents of the oospore.

Schreiber ((191) p. 358) has shown that in *Gonium* two of the

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[1] In *Gonium* this membrane is formed in the way above described for *Chlorogonium oogamum* ((191) p. 355).

[2] In rare cases some or all of these are also developed as swarmers (cf. fig. 28 D).

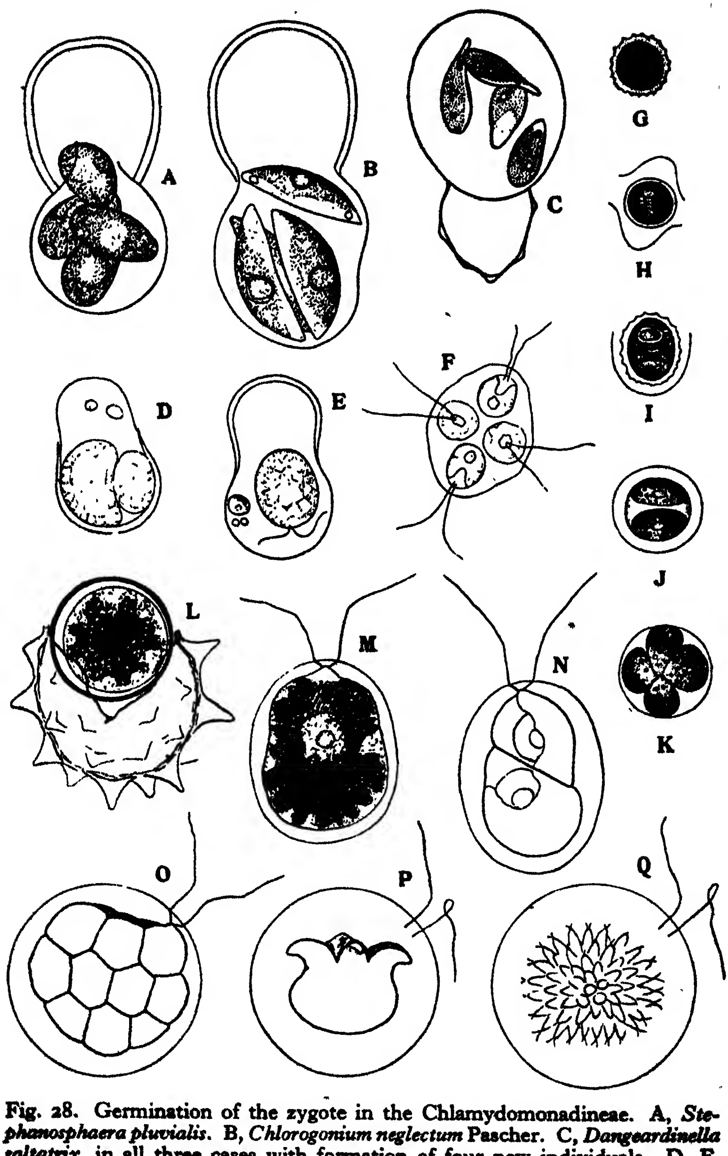

Fig. 28. Germination of the zygote in the Chlamydomonadineae. A, *Stephanosphaera pluvialis*. B, *Chlorogonium neglectum* Pascher. C, *Dangeardinella saltatrix*, in all three cases with formation of four new individuals. D, E, *Eudorina elegans*; D, abnormal; E, normal germination, note the abortive cells of the tetrad. F, *Gonium pectorale*, 4-celled coenobium formed from

coenobia formed from the 4-celled platelet of the zygote are of one and two of the other strain; zygotes were never obtained in cultures originating from a single coenobium and were in fact only formed when coenobia of different strain were brought together. In *Eudorina* ((191) p. 364) the coenobia formed from the single swarmer produced by the zygote are invariably unisexual. *Stephanosphaera* ((86), (193) p. 543) and *Chlamydobotrys* ((212) p. 686), on the other hand, are monoecious, although in the former according to Hieronymus only gametes from different parent-cells fuse. As regards the unicellular types, Strehlow ((212) p. 686) has shown that *Polytoma uvella* and some species of *Chlamydomonas* are monoecious, while a number of species of *Chlamydomonas* and *Chlorogonium* (cf. also (193) p. 543) are dioecious. In all these cases the zygote produces four or eight individuals. In view of the facts established for *Gonium* and for several of the advanced Chlorophyceae (cf. p. 44) it can hardly be doubted that, in the dioecious species, segregation of sex takes place during the reduction division in the zygote. Since occasional coenobia of *Eudorina* may be monoecious, it is clear that there may be some elasticity as regards the sex-segregation.

Everything tends to indicate that the ordinary vegetative individual in the Chlamydomonadineae is haploid. Pascher ((147) pp. 68, 293) and Korschikoff ((112) p. 485) have, however, drawn attention to some features which suggest the possible existence of diploid forms as well. In particular they instance certain species of *Chlamydomonas* (*C. pertusa*, *C. paradoxa*, *C. botryodes* ((212) p. 641)) in which the zygote remains motile for as long as ten days,[1] often assuming a special form (fig. 25 V); such zygotes give altogether the impression of independent individuals. In *Raciborskiella*, according to Wislouch (230), the zygotes divide to form a new colony without coming to rest. If this is correct, *Raciborskiella* is probably diploid. Pascher (154) has also described cases in which zygotes of *Dunaliella*, subjected to increasing salinity, gave rise only to two or to a single large *tetraflagellate* individual on germination. He suggests that the special external conditions had interfered with the reduction division and that the individuals produced were probably diploid.

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[1] In some cases these motile zygotes have been described as species of *Carteria*. Thus, the *C. ovata* of Jacobsen (91) is the zygote of *Chlamydobotrys*.

zygote. G–K, *Chlamydomonas Ehrenbergii*; G, zygospore; H, commencing germination; I–K, stages in tetrad-formation. L–Q, *Volvox Rousseletii* West; L, germinating oospore; M, swarmer liberated from same; N, first division of its protoplast; O, later stage of formation of new coenobium, before inversion; P, commencing inversion; Q, young coenobium ready to escape, but still within membrane of original swarmer. (A, B after Strehlow; C after Pascher; D–F after Schreiber; G–K after Goroschankin; L–Q after original drawings kindly furnished by Dr Pocock before the publication of her paper.)

Since the unicellular members of the Chlamydomonadineae frequently occur intermingled in large numbers, it is not improbable that hybridisation may occasionally occur. This may be responsible for the apparent intermediate types not uncommonly met with during the examination of large gatherings of *Chlamydomonas* and other genera. The artificial production of hybrids between species of *Chlamydomonas* has been accomplished by Pascher (143) and Strehlow ((212) p. 672). The former was able to follow the germination of a number of the hybrid zygospores which were intermediate in character between those of the parents (fig. 29 D–F). The offspring either resembled the latter in all respects or, in other cases, afforded a series of forms combining the characters of the parents in various ways, but so that of each pair of factors two individuals exhibited the one and two the other (fig. 29 G–J). Strehlow only succeeded in

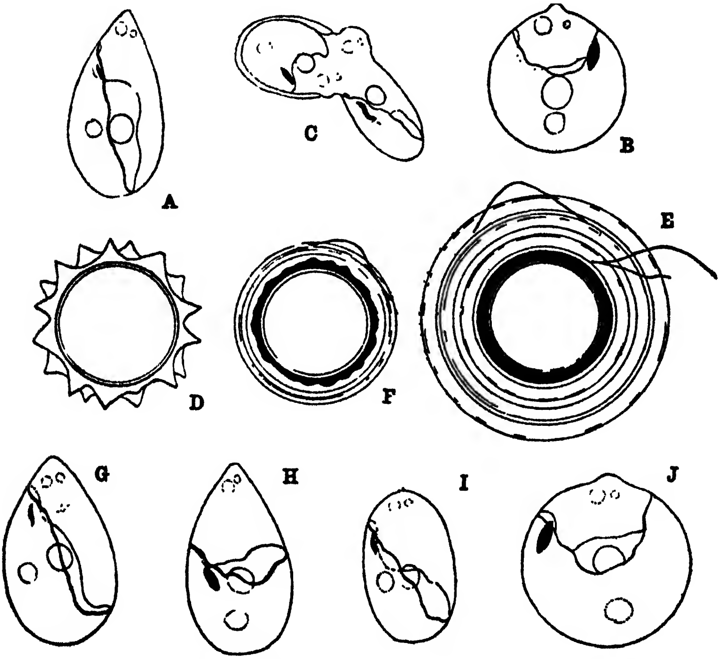

Fig. 29. Hybrids among species of *Chlamydomonas* (after Pascher). A, B, vegetative individuals of the two parents; D, E, their respective zygotes; C, fusion between gametes of A and B. F, the heterozygote. G–J, the four types of individuals obtained from the germination of one of the heterozygotes.

crossing the positive strain of *Chlamydomonas paradoxa* with the negative strain of *C. botryodes*.

(*b*) THE PALMELLOID FORMS (SUBORDER TETRASPORINEAE)

While among most Chlamydomonadineae the motile habit is altogether dominant, we find indications of another tendency in the palmelloid stages discussed above (p. 94). It is no doubt this tendency that has led to the evolution of the Tetrasporineae, and from this point of view a better knowledge than at present exists of the special factors calling forth the appearance of *Palmella*-stages is much to be desired. In the majority of cases these stages are only observed occasionally and are probably of brief duration, but species are known (e.g. *Chlamydomonas Kleinii*, fig. 16 P) in which apparently they become the dominant condition. From these it is but a slight step to the colonial Tetrasporineae in which motility occurs only in connection with reproduction, and the cells, which are always provided with a membrane, are held together solely by the mucilage in which they are embedded.

An interesting connecting link is furnished by *Chlorophysema* ((2), (147) p. 476) (fig. 30 G), the cells of which normally occur singly in a wide mucilage-envelope, sometimes attached by a definite mucus-stalk. After successive longitudinal division of the protoplast, from 2 (fig. 30 I, J) to 32 biflagellate swarmers provided with a membrane are set free and, after a brief period of movement, these settle down by their anterior ends to form a new individual. The swarmers may, however, fail to form flagella and constitute aplanospores (p. 41) with a gelatinous membrane and these may multiply in the same way to form palmelloid stages of some size (fig. 30 F).

A certain number of the Tetrasporineae, in which the four division-products of a parent-cell commonly remain grouped together and structures known as pseudocilia (cf. below) are present, appear to form a natural family, the Tetrasporaceae. But it is also convenient to include in the Tetrasporineae a number of other genera lacking these precise characteristics, but in which the cells are loosely embedded in copious mucilage. It is unlikely that these Palmellaceae constitute a natural assemblage, and the possibility of some of them being reduced forms must be kept in mind; many genera formerly placed here have now found a position elsewhere. In most Tetrasporineae the cells have a definite "chlamydomonad" structure (p. 79) and there is usually a pyrenoid in the basin-shaped chloroplast (fig. 30 D), but there are a number of aberrant types among the

Palmellaceae (cf. *Asterococcus* below) which may in the further course of research be found to be wrongly included here.

THE FAMILY TETRASPORACEAE

Tetraspora (176), the commonest genus of this family, usually occurs as indefinitely expanded (*T. gelatinosa*) or more or less tubular convoluted light green masses (*T. lubrica*), plainly visible to the naked eye and frequently found in stagnant waters in the spring, at first probably always attached, but later free-floating. The cells are embedded in a single layer in mucilage which is very soft and fragile. There are also known two planktonic species in which the colonies are microscopic and spherical (e.g. *T. limnetica*, fig. 30 A). The characteristic grouping of the rounded cells in fours (fig. 30 B) results from frequent division along two longitudinal planes at right angles to one another; individual cells or cell-groups are often surrounded by a special sheath of mucilage. From the outer surface of each cell a pair (sometimes four)[1] of fine thread-like processes arise, extending up to the surface of the mucilage (fig. 30 D, *p*) and often apparently projecting far beyond it ((66) p. 174, (104) p. 292). These pseudocilia (192), which can sometimes only be recognised after staining, consist of a delicate protoplasmic thread connected with the protoplast of the cell; a special sheath of denser mucilage is often recognisable around each pseudocilium (66).

The not uncommon freshwater epiphyte *Apiocystis* (35, 134) has small, usually pear-shaped colonies with a denser and well-defined superficial layer to the mucilage (fig. 31 A). In older colonies the cells divide in more than two directions, so that their arrangement becomes irregular, although they are usually found in a single layer. The paired pseudocilia (fig. 31 E) project markedly from the surface of the mucilage and, after staining, the gelatinous envelope around the central protoplasmic thread is very evident.

Schizochlamys gelatinosa (180) forms extensive, somewhat botryoidal, gelatinous masses in ponds, the contained cells being quite irregularly disposed. The cell-wall is firm and separated from the protoplast by intervening mucilage (fig. 31 C, *mu*). During division, or occasionally without division of the protoplast, the wall undergoes fracture into four fragments which persist in the surrounding mucilage (fig. 31 B). The protoplast exhibits a slight flattening or depression at the anterior end (fig. 31 C) and from this point there arise four protoplasmic processes (only two visible in the figure) which pass out of four pores in the membrane and each of which immediately branches into four delicate, radiating pseudocilia ((149) p. 445) without a special envelope (*c*); most of these pseudocilia are of great length. Scherffel has recorded the

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[1] According to Pascher ((149) p. 444, footnote).

presence of two contractile vacuoles (fig. 31 C, *v*) in the cells, a feature also seen in *Chlorophysema* (fig. 30 G) and in both cases indicating but a slight departure from the motile condition.

Recently Pascher (149) has described a genus *Porochloris*, epiphytic on *Sphagnum* and diverse filamentous Algae, which appears to be a close ally of *Schizochlamys*. As in the latter genus, there are four pores

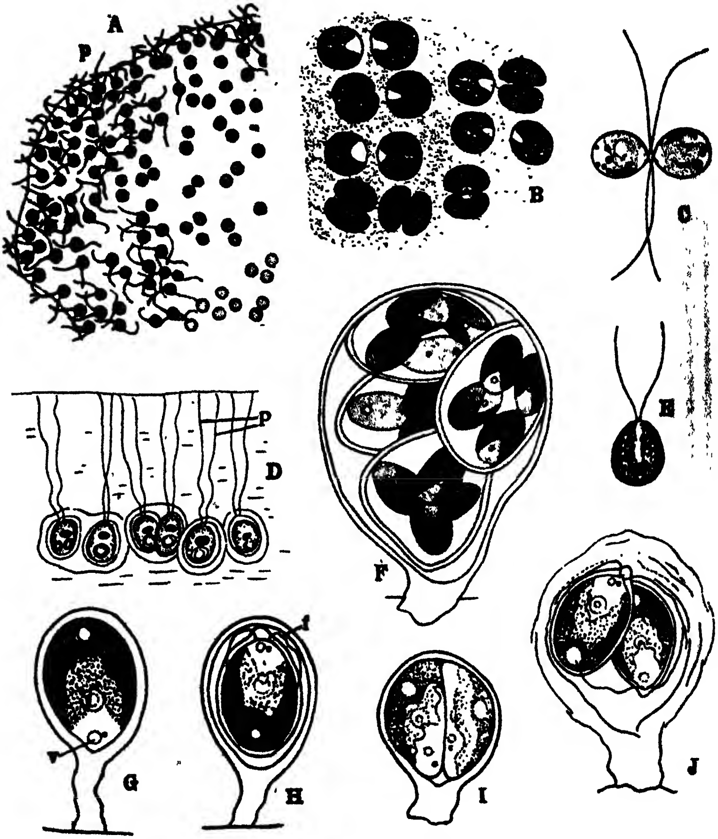

Fig. 30. A, *Tetraspora limnetica* West, part of a colony, with pseudocilia (*p*). B, C, E, *T. lubrica* (Roth) Ag.; B, arrangement of cells; C, sexual fusion; E, swarmer. D, *T. cylindrica* (Wahlenb.) Ag., with pseudocilia (*p*). F–J, *Chlorophysema apiocystiforme* Pascher; F, large colony; G, one-celled stage; H, formation of one and J, of two swarmers; I, division of protoplast. *f*, flagella; *v*, contractile vacuole. (A after West; B, E after Reinke; C after Geitler; D after Chodat; F–J after Pascher.)

in the coarse membrane, which is commonly encrusted with ferric hydroxide, and through each pore there passes a pseudocilium (fig. 31 I, *c*) which immediately divides into four. But in *Porochloris* the pseudocilia emerge at the four corners of the cell which is usually quadrangular in outline when viewed from the surface (fig. 31 I). There is also resemblance between the two genera in the fact that the protoplast of the epiphyte retains for some time the two contractile vacuoles and the stigma of the *Chlamydomonas*-like zoospores by means of which it reproduces; these are formed to the number of two or four from the cell-contents.

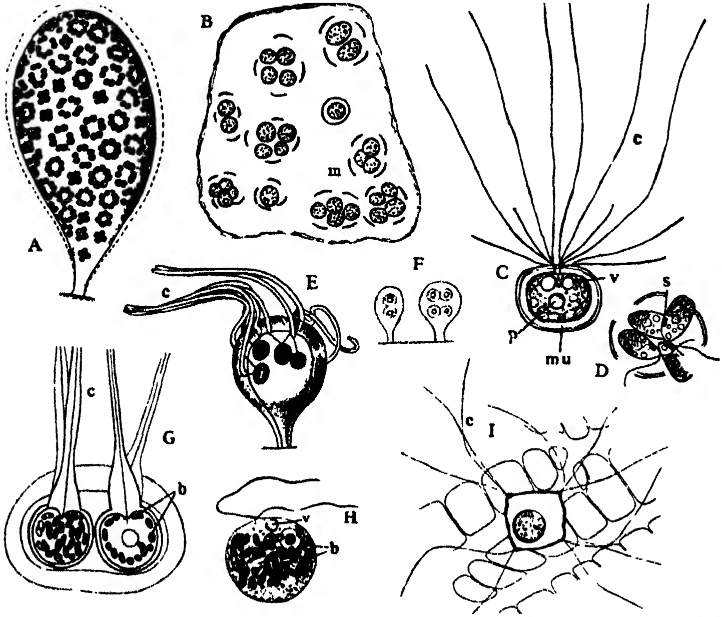

Fig. 31. A, E, F, *Apiocystis Brauniana* Naeg.; A, typical colony; E, young colony with pseudocilia (*c*); F, early stages in development. B–D, *Schizochlamys gelatinosa* Br.; B, part of stratum; C, single cell, the pseudocilia (*c*) actually much longer; D, swarmer-formation. G, H, *Gloeochaete Wittrockiana* Lagerh.; G, two cells with pseudocilia (*c*) clothed in a mucilage-sheath; H, swarmer. I, *Porochloris tetragona* Pascher. *b*, blue-green symbionts; *c*, pseudocilia; *m*, membrane; *mu*, mucilage; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (A, F after Naegeli; B after Frémy; C, D after Scherffel; E after Correns; G, I after Pascher; H after Korschikoff.)

A remarkable member of this family is constituted by *Gloeochaete*, long referred as an anomalous genus to the Myxophyceae, but now known to represent a colourless Tetrasporaceous form in which the blue-green "chromatophores" are symbiotic Blue-green Algae (63, 148). Each cell bears a pair of conspicuous pseudocilia which project for a long way beyond the common mucilage that encloses small groups of the cells (fig. 31 G); the gelatinous envelope of the pseudocilia is very strongly developed. Multiplication is effected by typical biflagellate swarmers (fig. 31 H).

The name pseudocilia is an unfortunate one, as these structures are not functionally of the nature of cilia or flagella; they are quite motionless and, when swarmers are produced, they are discarded. In part they appear to be mucilaginous in nature ((149) p. 434). They may aid in gaseous exchange, a view which receives some little support from their projection in *Apiocystis* where the surface-mucilage is especially firm.

THE FAMILY PALMELLACEAE

It must suffice to mention a few members of this family. *Palmella* and *Gloeocystis* form irregular gelatinous masses containing numerous cells, the former with structureless, the latter with stratified mucilage. The stratification in *Gloeocystis* (fig. 32 A, C) is due to the persistence of successive dilated mother cell-membranes, the daughter-protoplasts after division, as in all Tetrasporineae, forming new walls distinct from that of the parent-cell. The majority of the species of both genera are under suspicion and probably represent palmelloid stages of other Algae, but a few seem to be independent forms. Of these, special mention may be made of *Palmella miniata* ((21) p. 587) (fig. 32 D), which forms brick-red gelatinous masses on damp substrata and in which the green colour of the chloroplasts of the globose cells is obscured by a red pigment, and of *Gloeocystis vesiculosa*,[1] found on damp soil and in stagnant waters. Mainx (125) has described a species of *Gloeocystis* in which the vegetative cells possess a stigma.

In *Palmodictyon* (including *Palmodactylon* of Naegeli (136)) the mucilaginous expanses are more definite, taking the form of branched cylindrical masses (fig. 32 F, G), in some species showing considerable anastomosis between the branches. Another remarkable form is the net-like *Tetrasporidium* (87, 132), at present only known from Tropical Asia, in which the cells of the colonies possess contractile vacuoles. In *Palmophyllum*, most of whose species are marine, the mucilage has the form of a delicate lobed foliaceous expanse which exhibits concentric stratification (fig. 32 B).

Sphaerocystis Schroeteri ((23); cf. also (161) p. 501) is a widely distributed planktonic alga with microscopic spherical colonies containing more or less numerous cells scattered rather sparsely in the

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[1] See (4), (62), (67), (136).

periphery of the very hyaline mucilage (fig. 33 A). The cells are ordinarily globose, but during active division oblong cells are formed. Division either takes place into two or tetrahedrally into four (fig. 33 A), and it is characteristic of the alga that the various cells divide at different times and to a varied extent so that, while some may be large and globose, others are much smaller and grouped in fours or larger aggregates.

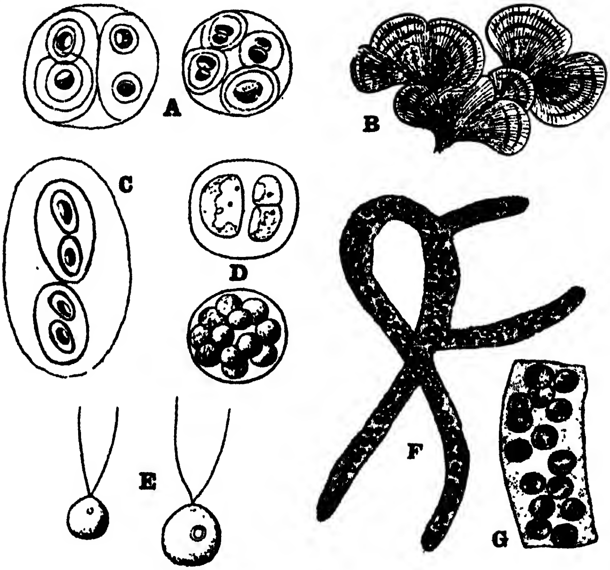

Fig. 32. A, C, *Gloeocystis Naegeliana* Artari (after Artari). B, *Palmophyllum crassum* (Nacc.) Rabenh. (after Kützing). D, E, *Palmella miniata* (Leibl.) Chod. (after Chodat); D, stage of division above, sporangial stage below; E, swarmers. F, G, *Palmodictyon varium* (Naeg.) Lemm. (after West); G, part of colony enlarged.

In spite of its abundance, however, considerable uncertainty attaches to this form. Wille (226) was of the opinion that it was identical with an alga described by A. Braun ((14), (15) p. 57) as *Gloeococcus mucosus* and apparently not subsequently recorded. This was found at the bottom of ponds as lobed or globular masses reaching the size of an apple, but as Braun distinctly states that all the cells of such colonies possessed a pair of very long flagella and exhibited a feeble motion within the mucilage, it seems more probable that *Gloeococcus* represents the *Palmella*-stage of some chlamydomonad form, analogous to *C. Kleinii*.

Reverdin ((177) p. 91) shows two short flagella-like structures arising from the anterior end of the cell in some of the individuals of the colony of *Sphaerocystis* he depicts. These are stated to be immobile, but they are very unlike the pseudocilia of Tetrasporaceae and suggest true flagella. Perhaps, therefore, *Sphaerocystis* itself is but a relatively permanent *Palmella*-stage of a *Chlamydomonas*. It has also been regarded as a state of the planktonic *Tetraspora lacustris* but this seems improbable.

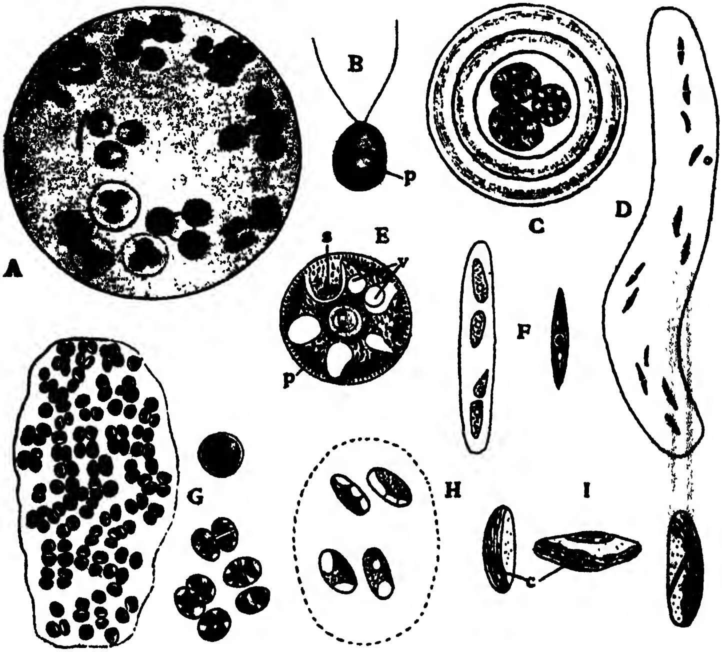

Fig. 33. A, B, *Sphaerocystis Schroeteri* Chod.; B, a supposed swarmer. C, E, *Asterococcus superbus* (Cienk.) Scherffel; E, single cell enlarged. D, F, *Elakatothrix gelatinosa* Wille; single cell on the right in F. G, *Pseudotetraspora marina* Wille; on the right a single cell (above) and cells in division (below). H, *Coccomyxa subellipsoidea* Acton. I, *C. dispar* Schmidle. *c*, chloroplast; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (A, B after Chodat; C, E after Scherffel; D, F, G after Wille; H after West; I after Schmidle.)

The rare *Rhodoplax*, recently investigated by Jaag (90), is a palmelloid form closely related to *Sphaerella* and like it storing abundant haematochrome in the cells. The swarmers differ in shape from the motile individuals of *Sphaerella*, but otherwise there is great general similarity.

While all the Palmellaceae hitherto described appear to possess cells with a chlamydomonad structure, there are some more aberrant types, such as *Coccomyxa* and *Asterococcus*. The former (90a, 189, 229) includes a number of terrestrial species in which the oval or spherical cells, usually embedded in mucilage, are often asymmetrical and provided with a lateral chloroplast which mostly lacks a pyrenoid (fig. 33 H, I). Certain species have been suspected of belonging to the Xanthophyceae (140), but according to the recent work of Jaag (90a) all the known forms are true Green Algae.[1] As shown by Chodat (25) and Jaag (90a) species of this genus are the gonidia of the lichens *Peltigera* and *Solorina*, while one species has been recorded in Ophiurids (cf. p. 189).

Asterococcus superbus (181), at one time regarded as a species of *Gloeocystis*, possesses relatively large, more or less globose cells occurring singly or in groups of 2–4 within concentrically lamellated mucilage-envelopes (fig. 33 C), reaching as much as 180μ in diameter. The chloroplast is axile and stellate with a central pyrenoid, its numerous processes extending up to the cell-wall, where they are slightly expanded (fig. 33 E). At one side of the cell (probably anterior) are found two contractile vacuoles (*v*) and a more or less distinct lanceolate stigma (*s*). Reproduction is effected by naked biflagellate zoospores formed singly from the entire cell-contents. In this ready assumption of motility and the possession of contractile vacuoles and stigma, *Asterococcus* shows that it is not far removed from a motile ancestry. No form with quite this kind of chloroplast is, however, at present known among Chlamydomonadineae.

In the case of two other genera, *Elakatothrix* (225) and *Pseudotetraspora* (227), the sole method of multiplication known is by division which is stated to take place after the manner of *Pleurococcus*, and Printz (170) therefore classes them in Pleurococcaceae. Both are incompletely studied and require further investigation. *Elakatothrix* is a plankton-form with rod- or spindle-shaped cells usually embedded in large numbers in hyaline mucilage (fig. 33 D, F), while in the marine *Pseudotetraspora* the cells are grouped in twos or fours at the periphery of a mass of mucilage which may attain considerable size (fig. 33 G); the parietal chloroplast is often stellately lobed.

Since the discovery of pseudocilia in *Schizochlamys* is comparatively recent, it is possible that these structures may yet be found in some of the Palmellaceae above discussed.

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[1] *Coccomyxa* should possibly be classed with the Chlorococcales, as advocated by Jaag (90a).

Reproduction of the Tetrasporineae

Apart from vegetative propagation by fragmentation of the colonies, the majority of the forms above considered are known to multiply by means of swarmers, usually biflagellate (figs. 30 E, 31 D, 32 E), though occasionally (*Schizochlamys*) quadriflagellate. The swarmers appear generally to be formed from the naked protoplasts of the ordinary cells which, after acquiring flagella, contractile vacuoles, and eye-spots, slip out of their membranes and the surrounding mucilage. After a period of movement they come to rest, secrete mucilage, and proceed to form a new colony. In *Schizochlamys* the swarmers arise by division of the contents of a cell into 2–8 parts (fig. 31 D) and the same may be true of other forms. In *Palmella miniata* and *Sphaerocystis* swarmers of two sizes have been recorded.

It appears that the motile cells do not in all cases give rise directly to a new colony. Under certain circumstances those of *Tetraspora*, for instance, divide to form palmelloid masses, differing from the normal colony in form, or they may give rise to resting stages with a thick brown wall ((24) p. 111). All the known facts relating to the asexual reproduction of the majority of the Tetrasporineae indicate a marked plasticity and emphasise their close relation to the free moving types. No motile reproductive stages are known in a number of genera (*Tetrasporidium*, *Palmophyllum*), but it is quite possible that they will yet be found. *Coccomyxa*, on the other hand, appears definitely to lack motile reproductive stages (90*a*),[1] the cells multiplying by division of the protoplast into a number of parts which become invested by new membranes of their own.

Sexual reproduction is only certainly established in *Tetraspora*, *Apiocystis* (134), and *Palmella miniata*, and is always isogamous. The biflagellate gametes are formed in some numbers (2–8 in *Tetraspora*) by successive division of the protoplasts of the ordinary cells. In the case of *Tetraspora lubrica* Geitler (66) finds that the colonies are strictly dioecious and that zygotes are only formed when gametes of opposite strains are brought together. The gametes, in which the chloroplast occupies a lateral position (fig. 30 C), aggregate in clumps. Those which fail to fuse show no further development. The zygote is stated to be capable of immediate germination. According to Klyver ((104) p. 294), after some enlargement, it gives rise to four or eight aplanospores from which collectively the new colonies originate.

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[1] Acton (1) recorded zoospores in *C. subellipsoidea*, but considerable doubt attaches to this observation (cf. (25) p. 224, (90*a*), (140) p. 211).

(*c*) THE DENDROID FORMS (SUBORDER CHLORODENDRINEAE)

One can regard Pascher's *Malleochloris* ((147) p. 480) as a very simple member of this suborder. This alga is found epiphytic on Cladophoraceae in the shape of small rounded cells attached by a short stratified mucilage-stalk (*st*), in which the lower part of the cell is embedded (fig. 34 A). The cells show chlamydomonad structure, the basal portion of the chloroplast with its pyrenoid facing outwards. In young individuals there is a distinct stigma (*s*). Reproduction is effected by longitudinal division of the protoplast into two (fig. 34 A) or four parts which are liberated as quadriflagellate swarmers (fig. 34 B). These become attached to a new substratum by their anterior end and rapidly form the mucilage-stalk. The contractile vacuoles evident in the swarmers seem to disappear. Isogamous sexual reproduction has also been observed with the formation of thick-walled zygospores. *Malleochloris* may be regarded as a *Carteria* which spends the greater part of its life in a sedentary condition. Other similar forms (*Stylosphaeridium* Geitler (64) (fig. 34 C)) are known, which approximate more closely to the epiphytic Chlorococcales (cf. *Characium*, p. 151), and there may well be some sort of relationship between them and the Chlorodendrineae.

In Stein's *Chlorangium* (28, 209), the species of which are found attached to Crustacea and Rotifers in freshwater plankton,[1] the spindle-shaped cells are likewise anchored by mucilage-stalks (fig. 34 F), but in this case, since the cells do not immediately resume the motile habit after cell-division, small branched colonies arise (fig. 34 D). The swarmers (fig. 34 E) are clothed in a cell-wall, are provided with two relatively short flagella, and are stated to be formed directly, by detachment of the ordinary cells of the colonies. They become fixed to the substratum by their anterior end which secretes a longer or shorter stalk (fig. 34 F). Sooner or later the protoplast divides longitudinally (or obliquely?), usually into two (fig. 34 G) but sometimes into four (fig. 34 I), the products acquiring new membranes of their own, after which the parent-cell membrane breaks open apically (fig. 34 H). The daughter-cells in their turn secrete mucilage-stalks basally, whereby they become attached to the persisting base of the parent-membrane and, as the stalks gradually elongate, the new units become carried out as branches of the stalk first formed (fig. 34 J). In this way small dendroid colonies arise. The mucilage-stalks are comparatively slender and occasional ones may attain some length. The cells possess a parietal chloroplast, which is in one or two pieces and devoid of a pyrenoid, and each exhibits at its lower (anterior)

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[1] A marine species is also known.

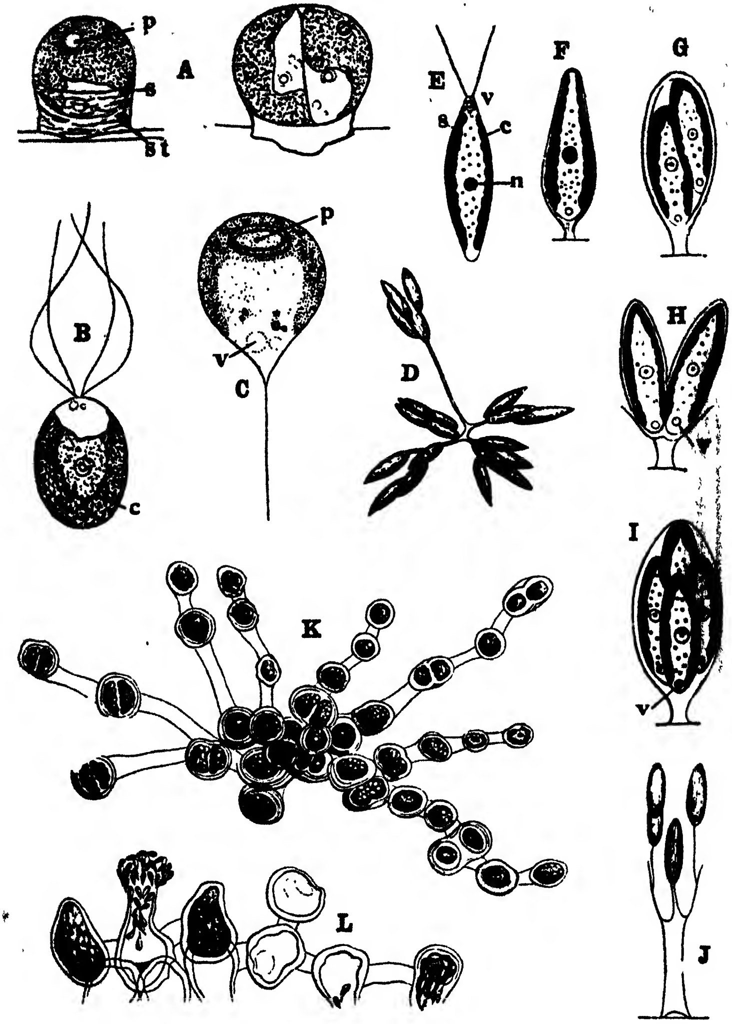

Fig. 34. A, B, *Malleochloris sessilis* Pascher (after Pascher); A, mature cell on the left, division-stage on the right; B, swarmer. C, *Stylosphaeridium stipitatum* Geitler (after Geitler). D–J, *Chlorangium stentorinum* (Ehrenb.) Stein (D, J after Cienkowski; the rest after Stein); D, colony; E, swarmer; F, attached cell; G–I, various stages in division; J, young colony. K, L, *Hormotila mucigena* Borzi (after Borzi); K, a large colony; L, formation of swarmers. *c*, chloroplast; *n*, nucleus; *p*, pyrenoid; *s*, stigma; *st*, stalk; *v*, contractile vacuole.

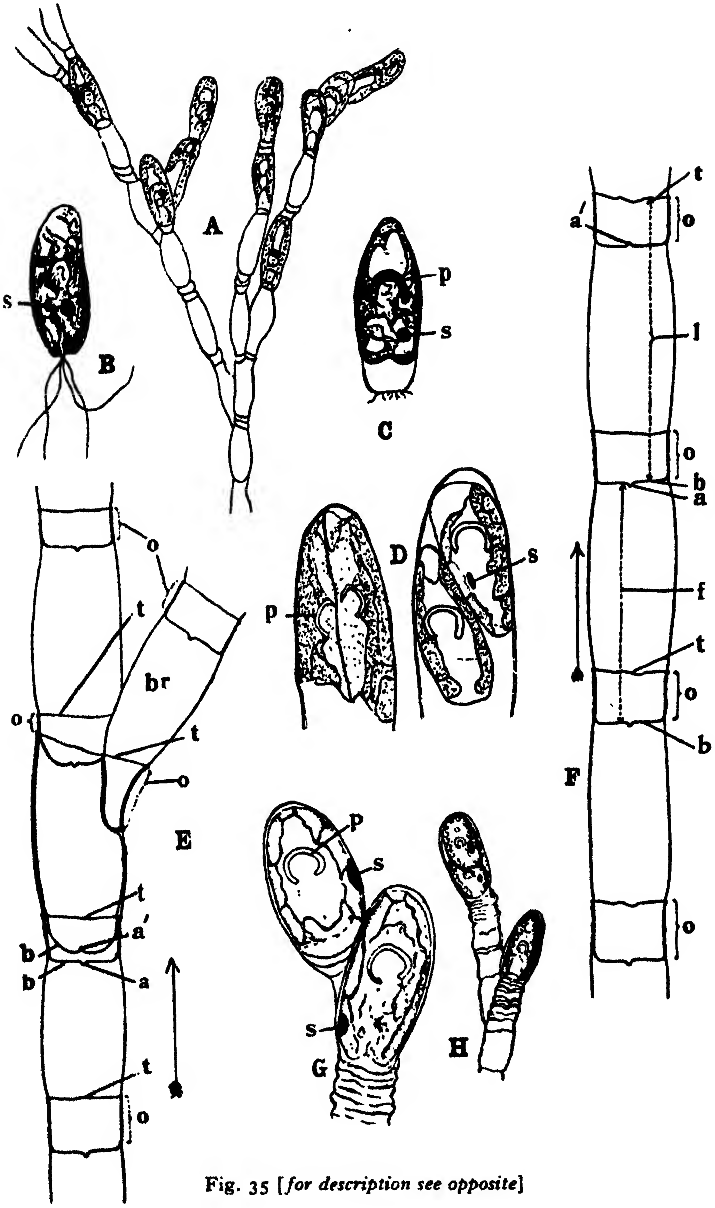

Fig. 35 [*for description see opposite*]

extremity a pair of contractile vacuoles (*v*). Jasnitzky (95) records gamete-formation in a Russian species.

The microscopic colonies of *Prasinocladus*[1] are formed in a somewhat different manner. This alga is commonly met with in aquaria containing seawater, but has also been found in the littoral zone and in brackish waters. The quadriflagellate swarmers (fig. 35 B) are again provided with a cell-wall; the single chloroplast, though somewhat dissected, is essentially of the chlamydomonad type, with a large polar pyrenoid (p. 68) and a well-marked stigma (*s*). After attachment to a substratum, the protoplast sooner or later secretes a completely new membrane, after which the apex of the original wall of the swarmer ruptures, and the contents shift upwards to a more or less marked extent (fig. 35 C), until the base of the new cell is only enclosed in a collar-like strip of the apex of the old cell-wall (fig. 35 E, F, *o*). The same series of events takes place repeatedly and thus the original protoplast may become carried up on a filament of increasing length, composed of empty membranes and showing numerous transverse septa (*b*, *t*) corresponding to the basal and terminal parts of the successive cell-walls formed by the protoplast. These septa stand close together or at more remote intervals, according to the degree of upward movement carried out by the rejuvenated cell on each occasion. At times the protoplast undergoes an oblique longitudinal division (fig. 35 D) and then one half may push out laterally to form a branch (fig. 35 E, G). It also happens, however, that one half-protoplast remains in the parent-membrane, while the other continues the growth of the filament, so that occasionally a protoplast is found occupying one of the often long series of empty chambers (fig. 35 A).

According to Lambert ((121) p. 239) the anterior (lower) end of the cell is provided with a papilla (fig. 35 E, F, *a*) and forms four flagella at each process of rejuvenation, although these flagella are soon withdrawn. This means that there is a successive formation of motile (walled) cells, any one of which might potentially become a free swarmer, and it would be of interest to ascertain what conditions

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[1] See (45), (117), (121), (234). This is the same as Senn's *Chlorodendron* (197) and Davis' *Euglenopsis* (48).

Fig. 35. Structure of *Prasinocladus*. A–C, *P. subsalsa* Davis (after Davis); A, part of a colony; B, swarmer; C, the same germinating. D, G, H, *P. lubricus* Kuck. (after Zimmermann); D, cell-division; G, H, branch-formation. E, F, *P. subsalsa* (?) (after Lambert), diagrams to explain mode of growth and branching of the colonies. *a*, papilla of wall; *a'*, abnormal papilla; *b*, basal wall of cell; *br*, branch; *f*, length of filament chamber; *l*, entire length of cell from wall *b* to terminal margin *t*; *o*, overlap of cell-walls; *p*, pyrenoid; *s*, stigma; *t*, terminal margin of cell.

determine whether the rejuvenated cell shall become free or shall be retained as the terminal cell of the filament. In any case *Prasinocladus* is clearly but little removed from a motile form, and in this connection it may be noted that the stigma remains recognisable in all the protoplasts of the colony, although, as in so many marine forms, contractile vacuoles are lacking.

The form originally described by Kuckuck (117) was, according to his own account, growing under rather unfavourable conditions and was characterised by the fact that the successive compartments of the filament were very short, so that the septa followed very closely upon one another (fig. 35 G, H). These filaments he interpreted as stratified mucilage-stalks. The later work of Zimmermann (234) has made it clear that Kuckuck's form belongs to the same genus as the *Chlorodendron* subsequently described by Senn, but it still remains doubtful whether the two forms belong to the same species, as there are certain differences in the shapes of the swarmers.

While *Chlorangium* and *Prasinocladus* are clearly closely related to the motile Chlamydomonadineae, this is not so evident in the case of other genera belonging to the Chlorodendrineae. *Ecballocystis* ((12) p. 7, (57) p. 494, (87)), which seems to be widely distributed in freshwaters (commonly flowing) in the southern hemisphere (Brazil, South Africa, India), but is also known to occur in Great Britain (59), does not so far as present evidence goes appear to reproduce by motile cells. Moreover, the cells contain more or less numerous parietal plate-shaped chloroplasts with pyrenoids (fig. 36 A, *c*), a rather unusual type among Volvocales. The colonies, which in some species are microscopic but in others form extensive gelatinous expanses, exhibit considerable differences in detail (fig. 36 B, F), but are essentially formed in the following manner. The reproductive cells, floated on to a suitable substratum, become attached by the secretion of a mucilage-cushion (*m*) at one end of the cell and gradually assume a more or less erect position ((87) p. 215) (fig. 36 C–E). Soon the protoplast divides more or less obliquely into two or more parts, which become enveloped by membranes of their own (fig. 36 H) and proceed to enlarge, whereby the wall of the parent-cell is dilated and ultimately broken open at its upper end (fig. 36 I). The daughter-cells then become fixed by basal mucilage-pads to the inner surface of the ruptured wall and, according to the exact positions which they take up, different types of colonies are produced (fig. 36 B, F). These have been described in detail by Iyengar who has been able to relate the different types to the elastic properties of the successive parent-cell membranes and the exact mode of division. Reproduction seems to be effected by the liberation of the contents of terminal cells, which usually divide into more numerous parts than in the ordinary divisions of the colony (fig. 36 J).

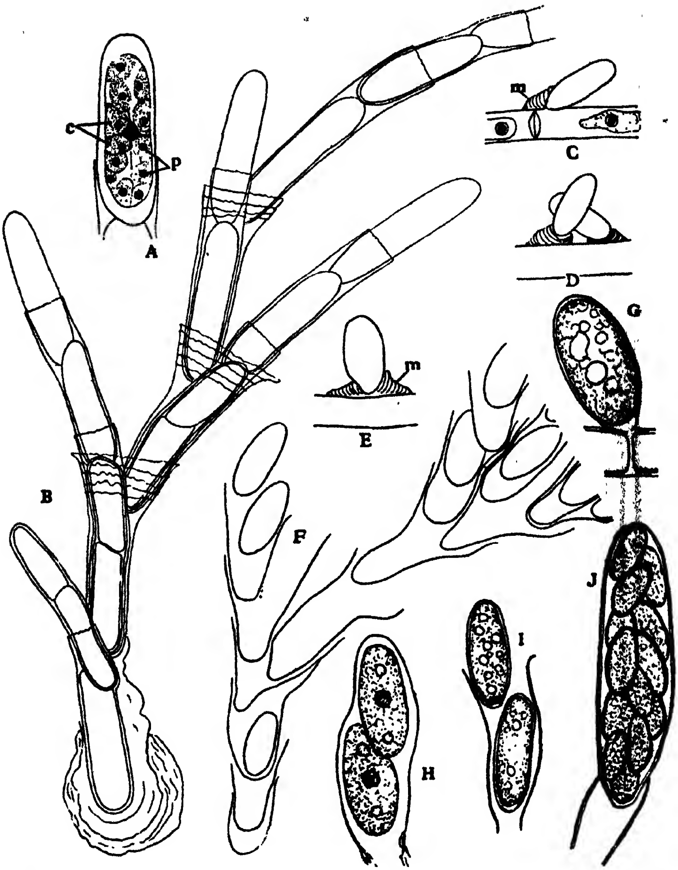

Fig. 36. Structure of *Echallocystis*. A, B, *E. courtallensis* Iyeng.; A, single cell; B, part of a colony. C–E, *E. ramosa* Fritsch, showing progressive erection of cells. F, *E. Fritschii* Iyeng., part of colony. G–I, *E. ramosa*; G, one-celled stage; H, completed division; I, rupture of parent-membrane. J, *E. simplex* Fritsch, sporangial cell. *c*, chloroplast; *m*, mucilage; *p*, pyrenoid. (G–J after Fritsch, the rest after Iyengar.)
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In *Echallocystopsis* (88) the division of the protoplast is practically transverse and the parent-membrane gelatinises completely except for the end-pieces which persist for a considerable time as a number of strata between consecutive generations. This results in a definite filamentous habit.

Hormotila mucigena Borzi ((13) p. 99) is a dendroid form, occasionally found on damp rocks and other similar substrata or attached to submerged objects (fig. 34 K). The spherical or ellipsoidal cells, which often possess thick stratified walls, are placed at more or less regular intervals in branched mucilage-cylinders, commonly showing concentric lamellation. The cell-structure is uncertain, some accounts speaking of a single chloroplast, others of a number of small ones. Biflagellate swarmers are formed in large numbers by the division of the contents of enlarged cells, from which they are liberated by a lateral rupture (fig. 34 L). This is the only member of the suborder in which the reproductive cells differ markedly from the vegetative ones.

The Chlorodendrineae are no doubt an artificial group, linked solely by the habit of forming dendroid colonies. Nothing, however, is to be gained by merging them in the Tetrasporineae, as is usually done. It is probable that the individual genera are more nearly allied to diverse members of the Chlamydomonadineae than to one another. Some, as has been pointed out, are evidently closely related to free-moving forms, as seen in the readiness with which motility is assumed and the frequent presence of stigma or contractile vacuoles in the sedentary cells. Others, like *Ecballocystis* and *Hormotila*, appear more remote, the former in the absence of swarmers, the latter in the possession of differentiated swarmers. In these respects they may be said to have advanced in the direction of the more definitely sedentary Chlorococcales.

CLASSIFICATION OF THE VOLVOCALES

The previous considerations will have shown that it is impossible to draw any sharp limit between the three suborders dealt with in the preceding pages. The majority of the Tetrasporineae are but little removed from the *Palmella*-stages of the Chlamydomonadineae, and the more typical members of the Chlorodendrineae are mere motile types which have acquired the habit of a temporary sedentary existence. In both series, however, the motile habit is reassumed with the greatest ease, often with little or no modification of the vegetative cells. The fact that these derived forms sometimes show chloroplasts of a special type does not speak against a close affinity, since considerable diversity in type of chloroplast is met with even among the Chlamydomonadaceae.

The outline classification appended below is intended to afford an oversight, and no further discussion of the principles involved will be attempted. All the motile forms can conveniently be classed in the four families Chlamydomonadaceae, Sphaerellaceae, Polyblepharidaceae, and Phacotaceae. There does not appear to be any valid reason for separating the colonial from the unicellular types.

(*a*) *Suborder Chlamydomonadineae.*

1. *Chlamydomonadaceae:* Brachiomonas, Carteria, Chlamydobotrys, Chlamydomonas, Chloroceras, Chlorogonium, Cymbomonas, Eudorina, Furcilla, Gonium, Hyalogonium, Lobomonas, Mastigosphaera, Oltmannsiella, Pandorina, Parapolytoma, Pascheriella, Phyllomonas, Physocytium (?), Platychloris, Platydorina, Platymonas, Pleodorina, Polytoma, Scherffelia, Scourfieldia, Sphaerellopsis, Spirogonium, Spondylomorum, Stephanoon, Tetrablepharis. Tussetia, Volvox (?), Volvulina.

2. *Sphaerellaceae:* Sphaerella (Haematococcus), Stephanosphaera, Volvox.

3. *Polyblepharidaceae:* Chloraster, Collodictyon (?), Dangeardinella, Dunaliella, Gametamoeba, Hyaliella, Medusochloris, Phyllocardium, Pocillomonas, Polyblepharides, Polytomella, Pyramimonas, Raciborskiella, Spermatozopsis, Stephanoptera (45, 207), Trichloris, Ulochloris.

4. *Phacotaceae:* Chlamydoblepharis, Coccomonas, Dysmorphococcus, Phacotus, Pteromonas, Thoracomonas ((110) p. 192, (207)).

(*b*) *Suborder Tetrasporineae:*

5. *Tetrasporaceae:* Apiocystis, Gloeochaete, Porochloris, Schizochlamys, Tetraspora.

6. *Palmellaceae:* Asterococcus, Chlorophysema, Coccomyxa, Elakatothrix (?), Gloeocystis, Palmella, Palmodictyon, Palmophyllum, Pseudotetraspora, Rhodoplax, Sphaerocystis, Tetrasporidium.

(*c*) *Suborder Chlorodendrineae:*

7. *Chlorodendraceae:* Chlorangium, Ecballocystis, Ecballocystopsis, Hormotila, Malleochloris, Prasinocladus, Stylosphaeridium.

LITERATURE OF VOLVOCALES

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Order II. *CHLOROCOCCALES*[1]

Chlorococcum and Chlorella

Among the unicellular Chlamydomonadineae asexual reproduction of the individual is often preceded by withdrawal of the flagella and cessation of movement. If this brief motionless phase become indefinitely prolonged at the expense of the period of free movement, in other words if the swarmer come to rest soon after its liberation and remain passive during a prolonged period of vegetative growth before renewed production of motile cells takes place, we should have realised all the essential features of a simple member of the Chlorococcales, such as *Chlorococcum* (fig. 37 A, E; cf. also fig. 3 F, p. 14). *C. humicolum* (Naeg.) Rabenh.[2] is a common soil alga, also found on other terrestrial substrata, whose spherical cells possess much the same internal structure as a *Chlamydomonas*, although stigma and contractile vacuoles are lacking. The chloroplast is a parietal, almost spherical shell (figs. 3 F, 37 D), with an aperture of varying width at one side of the cell, a single pyrenoid often being embedded in the opposite side of the sphere. This structure is typical of many Chlorococcales and for the sake of brevity may be briefly designated "*chlorococcoid*". In the older and larger cells (fig. 37 E) several pyrenoids (*p*) occur. Some of the older cells may accumulate a yellow oil in which a bright red pigment is often dissolved which renders the structure obscure. Such cells represent resting stages. The adult cells gradually become multinucleate (fig. 37 E).

When the ordinary cells have reached a certain size successive division of the protoplast into two, four, eight, etc., parts takes place (fig. 37 A, G), each acquires an ovoid or oblong shape and two flagella (fig. 37 B), and then by rupture of the membrane these *naked* swarmers (zoospores) (fig. 37 F) are set free; at their first liberation, as in many filamentous Algae, they are often surrounded by a delicate vesicle which in a few seconds disappears. After a period of movement the flagella are withdrawn, the zoospore rounds off and, with the formation of a cell-membrane, a new vegetative phase is initiated. When several swarmers settle down close together, the resulting cells form a stratum, in which the individuals are often of very unequal size and frequently become angular as the result of mutual pressure (fig. 37 A). In some cases the swarmers behave as gametes (fig. 37 H), producing a spherical zygote which becomes the new individual; according to Puymaly (174, 175) the fusing swarmers are often of

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[1] This corresponds to the Protococcales of Oltmanns, Brunnthaler, etc. Since *Protococcus*, if the name be retained at all, is not a member of this order, the old designation should be abandoned.

[2] See (11), (21), (75), (221) p. 105.

unequal size.[1] The fact that apparently the same swarmers can develop independently or behave as gametes indicates a low stage of development, and such a state probably obtains in many of the simpler Chlorococcales. It may be noted in this connection that no case of oogamy has been reported in this order.

In studying the life-history of species of *Chlorococcum* production of aplanospores (fig. 37 A) has often been observed, although it is not known how readily this occurs in nature. These "arrested swarmers" (cf. p. 41) are often formed in considerable numbers, and it appears that the phenomenon may be repeated for more than one generation, with the development of palmelloid stages ((21) p. 478) whose cells may ultimately fall apart and resume the normal vegetative phase or be liberated as swarmers. In any case the aplanosporic state of

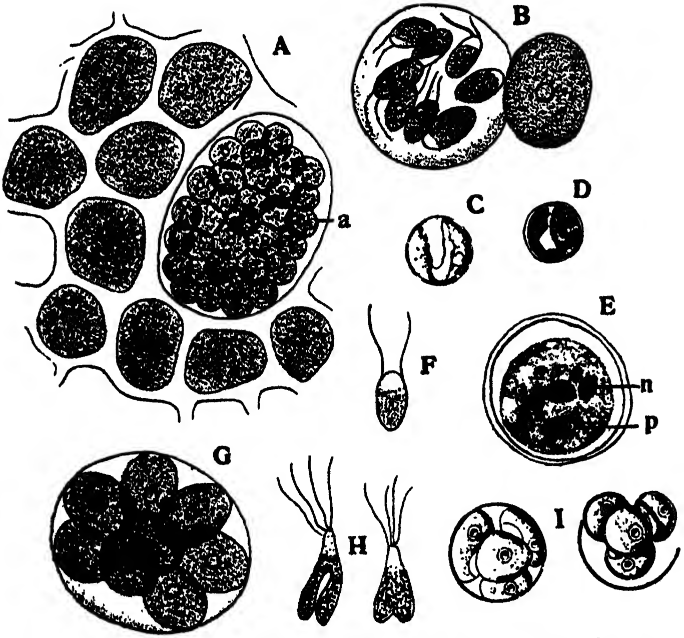

Fig. 37. A, B, D–H, *Chlorococcum humicolum* (Naeg.) Rabenh.; A, group of crowded cells, one with aplanospores (*a*); B, G, swarmer-formation; D, young, and E, older cells; F, swarmer; H, fusion of swarmers. C, I, *Chlorella vulgaris* Beij.; C, single cell; I, stages in division. *n*, nucleus; *p*, pyrenoid. (D, E, H after Bristol; C, I after Grintzesco; the rest after Beijerinck.)

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[1] Much the same life-history is reported by Bold (14) for another species, *C. infusionum*, although he did not observe sexual fusion (cf. also (204)).

Chlorococcum plainly shows the manner of evolution of such a form as *Chlorella* (75, 80) where new individuals are always formed straight away within the parent cell and swarmers are never produced (fig. 37 C, I). This is in fact the only feature that clearly distinguishes the two genera, although the cells are usually smaller than those of *Chlorococcum*. A certain number of Chlorococcales produce swarmers like *Chlorococcum*, but a much larger number seem to lack them and to reproduce after the manner of *Chlorella*. Such a contrast between zoosporic and azoosporic forms is met with in all the coccoid series of the Algae.

Brunnthaler (28) employed this feature in the classification of the order, the Chlorococcales being grouped into Zoosporinae (zoosporic forms) and Autosporinae (azoosporic forms). Oltmanns (149) and others have adopted much the same principle. Whilst such a grouping is convenient for systematic purposes it no doubt obscures affinities (cf. (72)), since it is probable that complete suppression of motility occurred again and again along different evolutionary lines. This matter will be further discussed later, but it is well to bear in mind that the Chlorococcales are almost certainly polyphyletic. They are essentially freshwater forms with a very manifold development, especially in the plankton. They appear to be entirely lacking in marine plankton (153).

THE UNICELLULAR CHLOROCOCCALES

The genus *Hypnomonas* of Korschikoff (110) differs principally from *Chlorococcum* in the presence of a pair of contractile vacuoles in the hyaline protoplasm at one side of the cup-shaped chloroplast (fig. 38 C). The biflagellate swarmers (fig. 38 G) have a delicate membrane, a lateral chloroplast, and a stigma which disappears when they come to rest. Here too aplanospore-formation may take place with the production of palmelloid phases. This form obviously constitutes a connecting link between *Chlorococcum* and the Chlamydomonadaceae.[1]

Other unicellular members of the Chlorococcales possess a somewhat different structure. *Trebouxia* (*Cystococcus* of Treboux, Chodat, etc., cf. (39), (174), (210), (221) p. 106), a not uncommon terrestrial form which constitutes the algal partner of many Lichens (cf. p. 183), possesses thin-walled spherical cells with an axile, massive chloroplast, produced into more or less well-marked lobes and harbouring a central pyrenoid; the nucleus is situated between two lobes of the chloroplast (fig. 38 D). The methods of reproduction appear to be

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[1] The fact that the swarmers are provided with a membrane renders them indistinguishable from a *Chlamydomonas* and it is really only the prolonged quiescent stage that turns the balance in favour of Chlorococcales.

quite similar to those of *Chlorococcum* (cf. fig. 38 A, B), although when a constituent of the lichen-body *Trebouxia* only forms aplanospores. Jaag ((95) p. 101) has observed a copulation of similar or dissimilar biflagellate gametes (fig. 38 H, I) in pure cultures of the gonidia taken from species of *Parmelia*.

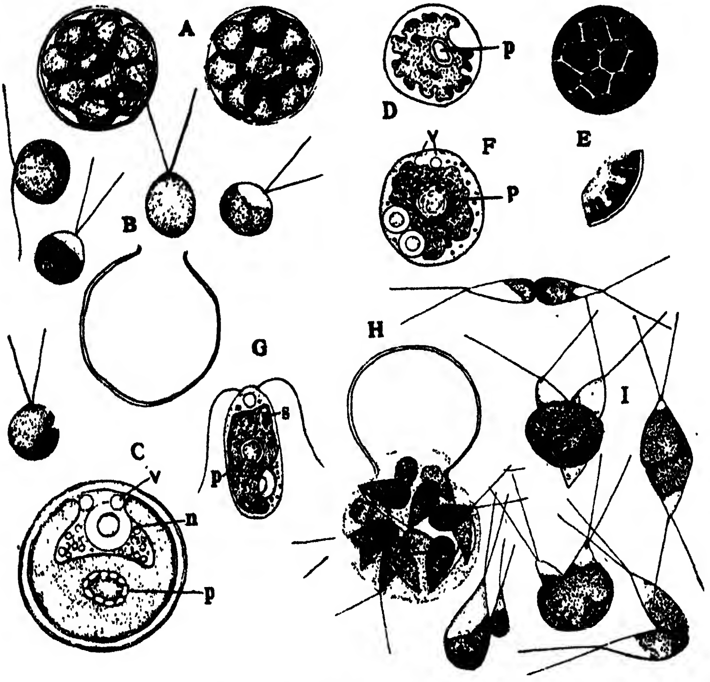

Fig. 38. A, B, H, I, *Trebouxia Parmeliae* Chod. (after Jaag); A, B, formation and liberation of zoospores; H, I, formation of gametes and sexual fusion. C, G, *Hypnomonas chlorococcoides* Korschik. (after Korschikoff); C, cell in optical section; G, swarmer. D, *Trebouxia humicola* Treboux (after Chodat). E, *Dictyococcus varians* Gern. (after Gerneck), the lower figure showing part of the chloroplast in optical section. F, *Apiococcus consociatus* Korschik. (after Korschikoff). *n*, nucleus; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole.

Korschikoff (110) describes a similar aquatic form under the name of *Apiococcus* which, like *Hypnomonas*, is characterised by the presence of a pair of contractile vacuoles in the ordinary vegetative cells (fig. 38 F). The swarmers behave as gametes, the resulting zygote giving rise directly to a new vegetative individual.[1] *Borodinella* (135 a)

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[1] It may perhaps be doubted whether there are sufficient differences to warrant a generic separation from *Trebouxia*.

is an allied type with a similar cell-structure in which groups of cells arranged tetrahedrally cohere to form larger colonies.

In other genera the chlorophyll-apparatus consists of several or numerous parts. In Gerneck's *Dictyococcus* (75, 162) there are a number of parietal lenticular or polygonal plates without pyrenoids, sometimes bearing short processes on their margins which extend into the interior of the cell (fig. 38 E). The swarmers are formed in large numbers by simultaneous division of the contents and aplanospores are also known.[1] In *Eremosphaera viridis* (132, 137), which is widely distributed, especially in *Sphagnum*-bogs, the large thin-walled spherical cells harbour numerous chloroplasts occupying the parietal cytoplasm, as well as the centrally directed protoplasmic strands (fig. 39 A). The individual chloroplasts vary somewhat in shape, but each possesses a conical projection directed towards the centre of the cell and encloses from 1–4 pyrenoids. Under one-sided illumination the chloroplasts accumulate on the side adjacent to the source of light (188). No formation of swarmers has ever been observed in this case, multiplication being effected by division of the protoplast into 2–4 parts which, after secreting membranes, are set free as new individuals (fig. 39 C, D). Reichardt (178) records the formation of as many as 16 aplanospores. The two forms just mentioned, and especially *Eremosphaera*, are clearly specialised types, but it may be recalled that even in *Chlamydomonas* forms are known with a number of discoid chloroplasts.

Other genera are characterised by complications in the structure of the membrane or in the shape of the cell. The species of *Micractinium* (including *Golenkinia* Chodat (32), *Richteriella* Lemmermann (125)) are planktonic forms, in the main distinguished from *Chlorella* by the fact that the firm cell-walls bear a number of variously disposed solid or hollow bristles which are outgrowths of the membrane (fig. 39 I). Reproduction takes place by aplanospores (fig. 39 H), and in some species the products of division remain together to form small loose colonies. A similar form is seen in *Borgea* (196) where, however, the cells are surrounded by a firm hyaline mucilage-envelope which is produced into a number of coarse tapering spines (fig. 39 J).

In *Trochiscia* (fig. 39 E–G) the spherical cells, found in quiet water or on damp ground, have a membrane ornamented in diverse ways (a network of ridges, spines, etc.), so that the cells resemble the resting stages of other Algae, or even the spores of higher plants. Many of the "species" of this genus are probably of this nature, but quite a number are known in which reproduction takes place after the manner typical for *Chlorella* ((221) p. 119, (226)) (fig. 39 F) and these are no doubt independent forms. In these the daughter-cells acquire all the

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[1] Petersen's *Muriella* (162) shows the same relation to *Dictyococcus* as *Chlorella* does to *Chlorococcum*.

characteristic markings of the parent before liberation, i.e. they are so-called autospores. The cell-structure appears to be chlorococcoid (p. 145), but older cells commonly contain several parietal chloroplasts with pyrenoids, perhaps as a preparation for division.

Tetraëdron (121, 144, 173, 203) has cells which are either flattened and

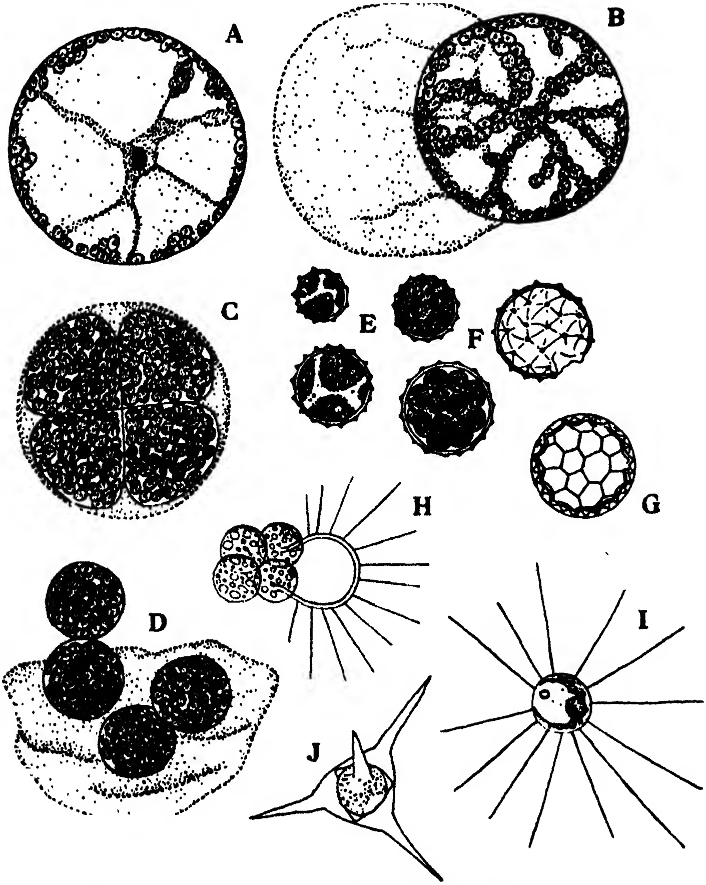

Fig. 39. A–D, *Eremosphaera viridis* De Bary (after Moore); A, cell in optical section; B, rejuvenescence; C, D, formation and liberation of daughter-cells. E, F, *Trochiscia aspera* (Reinsch) Hansg. (after West); F, development of daughter-individuals and, on the right, an empty membrane. G, *T. reticularis* (Reinsch) Hansg. (after West), membrane only. H, I, *Micractinium radiatum* (Chod.) Wille (after Chodat); H shows escape of aplanospores. J, *Borgea planctonica* Smith (after G. M. Smith).

angular or polyhedral, the angles commonly bearing simple or forked spines (fig. 40 A, B, H). In most cases the chloroplast appears to be a parietal curved plate, with or without pyrenoids, but there are also records of a number of chloroplasts (preparatory to division?). Many of the "species" of this genus are again under suspicion, as *Tetraëdron*-like stages are known to occur in the life-cycles of Hydrodictyaceae (cf. p. 173) and other Chlorococcales, while some may well be the resting stages of other Algae. For a number of species of *Tetraëdron*, however, reproduction by autospore-formation (fig. 40 C, D) has been established, the new individuals being formed by simultaneous division of the contents (195) (fig. 40, E–G); after being set free by rupture of the wall, they are often temporarily enclosed in a delicate vesicle.

A more peculiar form is constituted by *Desmatractum* (158)[1] in which the free-floating cells possess two envelopes, separated by a more or less wide space containing aqueous mucilage (fig. 40 I, J). The inner envelope is delicate and closely invests the usually spherical protoplast, whilst the outer is composed of two more or less pyramidal halves, joined together in the median plane and each provided with a number of longitudinal ridges. The protoplast possesses an essentially chlamydomonad structure and in young cells may exhibit a pair of contractile vacuoles. Reproduction is effected by the liberation of two or four biflagellate naked swarmers (fig. 40 K) or (perhaps more usually) by the formation of autospores; in either case the products escape by the gaping apart of the two halves of the membrane. The epiphytic *Octogoniella* (158), found on the green cells of *Sphagnum*-leaves, shows essentially the same structure. Here, however, the side of the cell which is apposed to the substratum is flattened (fig. 40 L), so that *Octogoniella* as it were corresponds to a longitudinally halved individual of *Desmatractum*. In this epiphyte reproduction by biflagellate swarmers is the rule, although aplanospores also occur. Another related form is possibly *Scotiella* (42, 69) (fig. 40 M, N), so far mainly found as a constituent of snow-floras.

A rather more specialised type is seen in *Characium* (19, 123, 183), in which the commonly ellipsoidal, oblong or fusiform cells are often asymmetrical, while they are invariably attached to a substratum by a short stalk expanded into a small basal disc (fig. 41 A–E). The parietal chloroplast which contains one or more pyrenoids is often rather diffuse ((193) p. 460). The ordinary method of reproduction is by means of biflagellate zoospores, which are formed by simultaneous or successive division of the protoplast (fig. 41 H, J) and are liberated through a terminal or lateral aperture.[2] In *C. limneticum* and *C. sacca-*

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[1] The same form has also been described under the names *Bernardinella* (41, 46, 111) and *Calyptrobactron* (71).

[2] Sometimes the swarmers settle down at the mouth of the empty mother-cell, forming small colonies (cf. (94)).

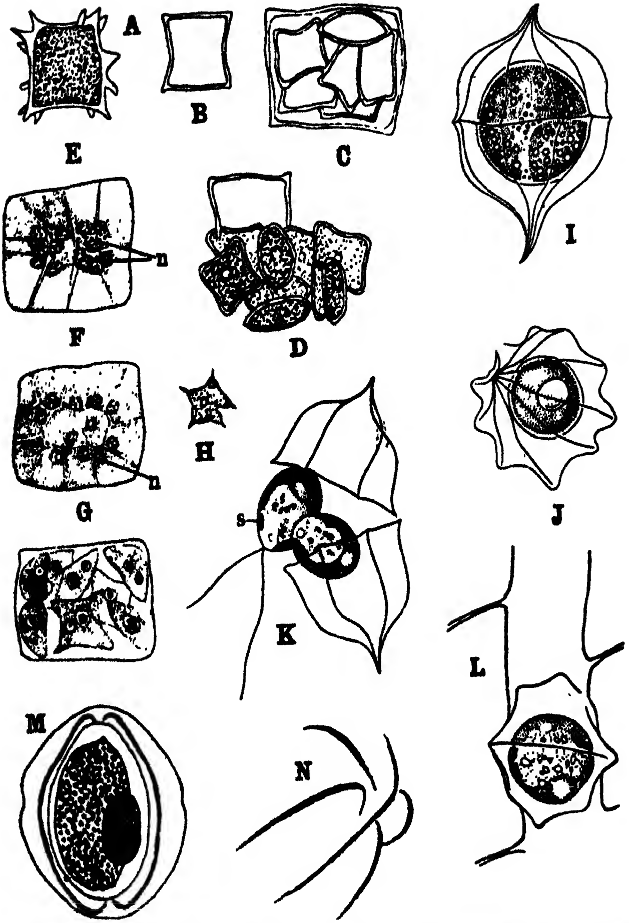

Fig. 40. A, *Tetraëdron horridum* West. B–G, *T. minimum* (A. Br.) Hansg.; C, D, formation and liberation of autospores; E, F, cleavage of the multinucleate protoplast; G, young autospores. H, *T. caudatum* (Corda) Hansg. I–K, *Desmatractum bipyramidatum* (Chod.) Pascher; I, cell from the side; J, oblique end-view; K, liberation of swarmers. L, *Octogoniella sphagnicola* Pascher, single cell on fragment of leaf of *Sphagnum*. M, N, *Scotiella antarctica* Fritsch; N, oblique end-view of the ribs. *n*, nucleus; *s*, stigma. (A after Printz; H after West; I, K, L after Pascher; J after Korschikoff; M, N after Fritsch; the rest after G. M. Smith.)

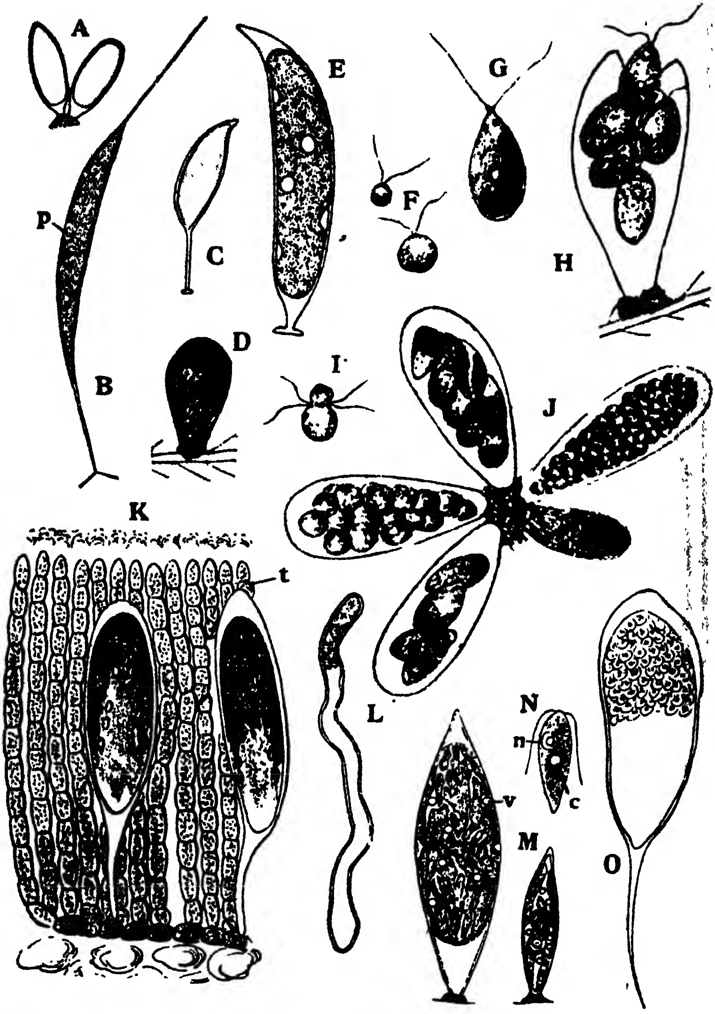

Fig. 41. A, *Characium Brunnthaleri* Printz. B, *C. gracilipes* Lambert. C, *C. longipes* (Rabenh.) Borzi. D, F–J, *C. saccatum* Filars.; D, young individual; J, group of individuals forming zoospores and gametes; H, liberation of zoospores; G, swarmer and F, gametes; I, sexual fusion. E, *C. apiculatum* Rabenh. K, O, *Codiolum petrocelidis* Kuck.; K, two individuals within the crust of *Cruoria*; O, swarmer-formation. L, *C. lacustre* Printz. M, N, *Characiochloris characioides* Pascher; N, swarmer. *c*, chloroplast; *n*, nucleus; *p*, pyrenoid; *t*, upright threads of *Cruoria*; *v*, contractile vacuole. (B after Lambert; D, F–J after Filarszky; K after Cohn; M, N after Korschikoff; O after Kuckuck; the rest after Printz.)

tum anisogamous sexual reproduction (fig. 41 I) has been recorded, and in the latter there are stated to be distinct asexual and sexual individuals, the latter producing micro- or macrogametes (67, 183). We are indebted to Pascher (157) for the discovery of a colourless species, while Korschikoff (114) has described forms in which numerous scattered contractile vacuoles are found in the cells (fig. 41 M, N). These are referred (114, 155) to an independent genus, *Characiochloris*, but the differences from the ordinary species of *Characium* are slight. Petrová's *Tetraciella* (163) has quadriflagellate swarmers.

Codiolum (19, 55 *a*, 98, 170),[1] the majority of whose species are marine, occurring on rocks near high-water mark, is a more highly differentiated type. The elongate and rather large cells possess an extensive parietal reticulate chloroplast containing several pyrenoids and bearing internally directed processes (98). Most of the species occur freely, but *C. petrocelidis* Kuckuck (116, 116 *a*) is an endophyte in the crusts (fig. 41 K) of various Florideae (*Petrocelis*, *Cruoria*, etc.). The quadriflagellate swarmers are formed by successive division of the cell-contents (fig. 41 O); they are pear-shaped with a pointed posterior end. Those of *C. petrocelidis* settle down on the surface of the host and put out a narrow rhizoïd which penetrates between the upright threads (fig. 41 K, *t*) of the latter. As these lengthen the *Codiolum* is gradually enveloped and ultimately completely buried. According to Zimmermann (231) during this process the cell-contents rotate through a right angle, so that the chromatophore of the swarmer comes to lie laterally. Subsequently both the rhizoid and the body of the original swarmer widen to form the more or less clavate mature cell, at whose apex the membrane is commonly specially thickened. Biflagellate swarmers (possibly gametes) are also known in certain species of the genus. There are considerable resemblances between *Codiolum* and *Protosiphon* (cf. p. 370).

THE ENDOPHYTIC HABIT AMONG CHLOROCOCCALES

The commonest of the endophytic genera, which are all zoosporic, is *Chlorochytrium*,[2] a form rather closely allied to *Chlorococcum*. The swarmers (fig. 42 C, D, sometimes zoospores, sometimes motile zygotes produced by sexual fusion) settle down on the surface of various aquatics, especially commonly on species of *Lemna*. After forming a membrane a tubular prolongation grows into the "host", either through a stoma or between two epidermal cells (fig. 42 B, *s*), and swells out within one of the intercellular spaces. Here it forms a large ellipsoidal, sometimes lobed cell which receives all the protoplasmic contents of the swarmer and slowly grows until a new re-

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[1] According to Jorde (235) the zygotes of *Urospora* develop into *Codiolum*-like stages (p. 241).

[2] See (20), (55 *b*), (68), (104), (170).

productive phase sets in (fig. 42 A, *r*). In the autumn the cells sink to the bottom with the dying *Lemna*-fronds, etc., and remain dormant until the spring. The wall of the resting cells is commonly thick and stratified and may exhibit local excrescences (fig. 42 F, G). The chloroplast in the mature cells of *C. Lemnae* (23) assumes a complex structure, apparently consisting of numerous parietal lobed plates or of an interrupted parietal layer, with a number of processes penetrating into the interior; according to Bristol ((23) p. 5) these processes radiate out from a central mass (fig. 42 F). Several pyrenoids are present (fig. 42 G, *p*).

In spite of the abundance of *Chlorochytrium Lemnae* its reproduction is not yet altogether clear. Biflagellate swarmers are produced to the number of 256 by successive division (fig. 42 H, I) of the contents of the endophytic cells and, according to Kurssanow and Schemakhanowa (119), the first two divisions are meiotic, so that the longest stage in the life-history is in this case a diploid one. The swarmers escape by rupture of the wall and of the surrounding tissues of the host, enclosed in a wide mucilage vesicle within which copulation apparently often occurs (fig. 42 E), although complete liberation prior to sexual fusion may also take place. The quadriflagellate zygotes (fig. 42 D) seek out a new host and penetrate into the interior in the way already described. This appears to be the normal course of the life-history and it seems that there may be several sexual generations in a single season. Liberation of the swarmers without fusion has, however, also been observed and such swarmers can likewise invade a new host; the Russian workers above cited are of the opinion that such swarmers are formed from haploid races that have arisen as a result of apogamy. It is commonly stated that swarmers which fail to reach a host perish, but it is doubtful whether this is of quite general application, since cells of *Chlorochytrium* have frequently been found in the soil (22, 139).

Apart from this species, which has also been observed as an endophyte in *Ceratophyllum demersum*, *Elodea canadensis*, and certain Mosses, a number of others are known.[1] These have in great part been referred to distinct genera (*Endosphaera*, etc.) in the past (cf. (104)), but the differences do not appear to be of generic value (23). *C. Cohnii* (*Chlorocystis Cohnii*) (136) and *C. Sarcophyci* (223) are found endophytic in diverse marine Algae (*Enteromorpha*, *Polysiphonia*, etc.), as well as in the tubular mucilage-envelopes of the Diatom *Schizonema*, the former also in lower animals.[2] For *C. Cohnii* Zimmermann (231) records quadriflagellate swarmers invading the host in the way above described,

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[1] Palm (152*a*) describes a "*Chlorochytrium*" forming small galls in the leaf of *Polygonum*, although it does not appear certain that the form involved is a green alga.

[2] An endophytic green alga, which is possibly a species of *Chlorochytrium*, has been reported in the skin of the carp (127).

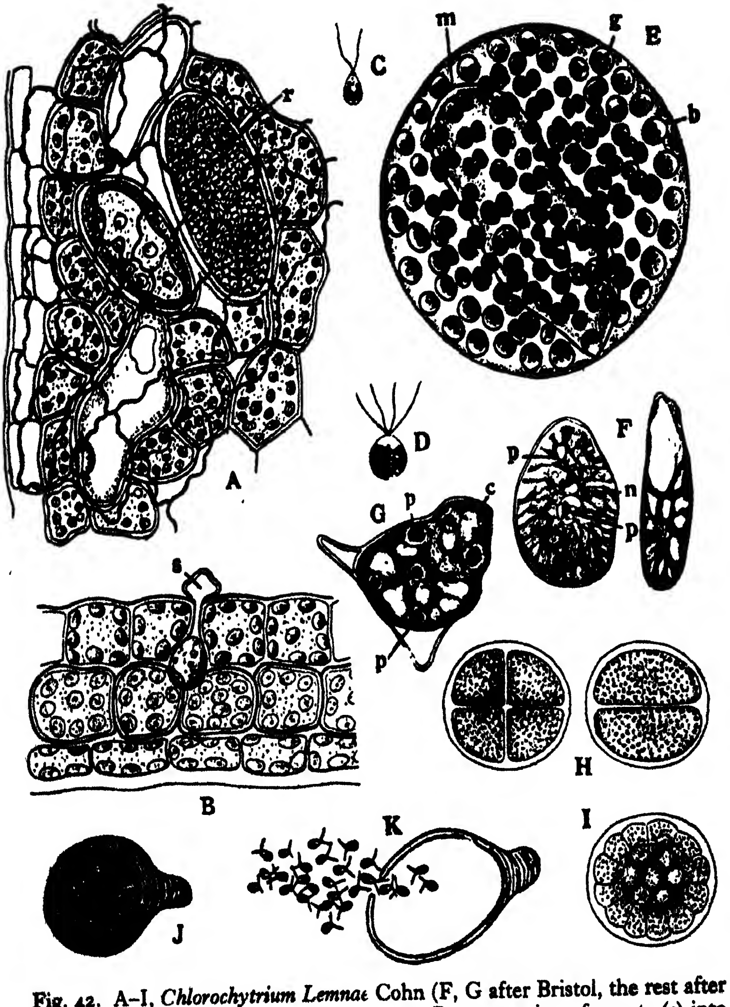

Fig. 42. A–I, *Chlorochytrium Lemnae* Cohn (F, G after Bristol, the rest after Klebs); A, resting cells (*r*) in leaf of *Lemna*; B, penetration of zygote (*s*) into host; C, swarmer; D, zygote; E, liberation of swarmers (*g*) into vesicle (*b*), the outline of the membrane (*m*) of the resting cell below; F, G, structure of resting cells; H, I, division-stages of same. J, K, *C. Facciolaae* (Borzi) Bristol (after Borzi); K, escape of swarmers. *c*, chloroplast; *n*, nucleus, *p*, pyrenoid.

the protoplasmic contents in passing into the interior rotating through 180°, so that the polarity of the swarmer is completely inverted. Another common species is *C. Facciolaae* (*C. gloeophilum* Bohlin (13, 138)), for which Printz ((171) p. 88) still maintains Borzi's genus *Kentrosphaera* ((15) p. 87; cf. also (178)); the resting cells, which show peculiar localised projections of the thick membrane (fig. 42 J, K) are commonly found among the filaments of diverse Oscillatoriaceae, as well as among those of marine Cladophoraceae.

A further development of the endophytic habit is seen in the genus *Phyllobium* (104), of which *P. dimorphum* Klebs forms its resting cells along the principal veins of the leaves of *Ajuga*, *Lysimachia*, etc., while *P. sphagnicolum* West (218) is found on *Sphagnum* (fig. 43 B). The former species has been studied in detail by Klebs. The vegetative body is composed of branched coenocytic threads (cf. fig. 43 C), which may exhibit occasional septa and which swell up at certain points to form elongate or globose resting cells (gametangia) (fig. 43 A, *g*). The latter accumulate all the protoplasmic contents of the threads and appear as bright green nodose swellings on the leaves of the host; in some cases they are coloured red by haematochrome. The chloroplast in these gametangia appears to be similar in structure to that of *Chlorochytrium*. The gametangia (fig. 43 D) either produce large macrogametes in limited numbers or more numerous microgametes, about half the size of the former; both are biflagellate. Sexual fusion (fig. 43 E) is stated always to occur between two dissimilar gametes, the microgamete being completely engulfed by the other, so that the zygote possesses only two flagella. In addition there are formed relatively small resting cells with a thick wall, which appear to arise directly from the tubular prolongation sent into the host by the swarmer, and these give rise to large biflagellate zoospores which germinate directly. In *P. sphagnicolum* the vegetative threads ramify through the pores in the leaf-cells of *Sphagnum*, the dark green resting cells being formed on the surface (fig. 43 B). The details of reproduction are not known in this case. *Phyllobium* is probably diploid, like *Chlorochytrium*.

Many authorities regard Lagerheim's *Rhodochytrium* (10, 78, 122), a parasite lacking chlorophyll, as representing a further evolution of this habit (cf. especially (171) p. 94). This form has been recorded in the leaves of various Phanerogams from different parts of the American continent, whence it has been introduced into Sumatra (152). The host does not appear to be appreciably damaged, although the phloem is locally destroyed (78). The frequent red colour of the threads of the parasite (fig. 43 F) is due to the presence of oil-drops containing a red pigment (probably haematochrome). As in *Phyllobium*, all the contents ultimately aggregate in a number of large spherical or irregular swellings (fig. 43 H) which produce biflagellate swarmers with a red anterior end (fig. 43 G). These are either isogametes or zoospores; according to Griggs they copulate only when there is a deficiency of water. In the later part of the season the swellings develop into resting cysts which, like other parts of the organism, harbour abundant starch. This genus shows certain resemblances to Chytridiales which may or may not be of significance.

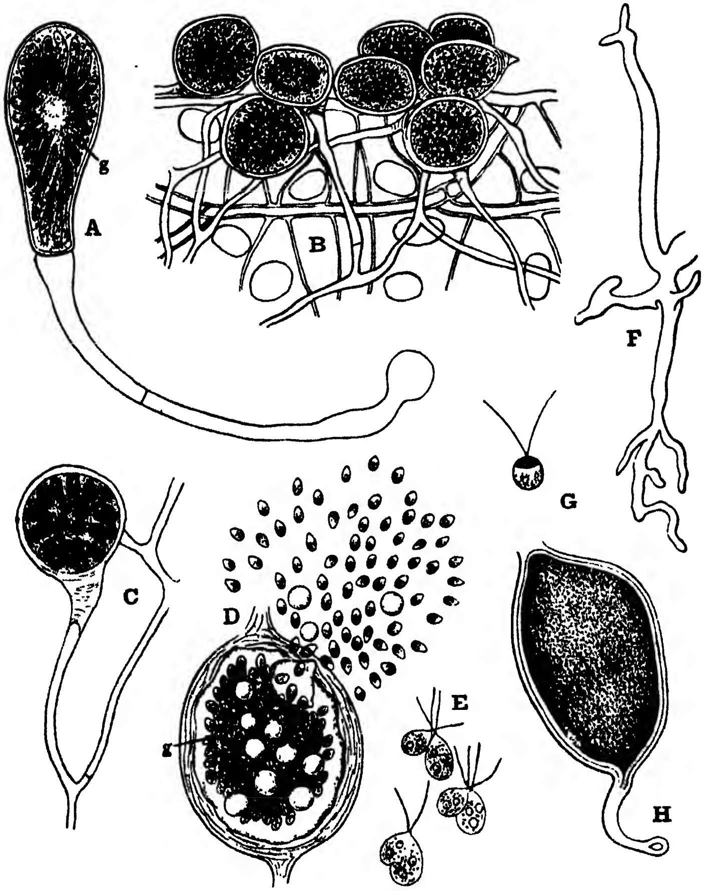

Fig. 43. A, D, E, *Phyllobium dimorphum* Klebs (after Klebs); A, gametangium (*g*) at the end of an empty thread; D, liberation of gametes; E, sexual fusion. B, C, *P. sphagnicolum* West (after West); B, resting cells on *Sphagnum*-leaf; C, structure of chloroplast. F–H, *Rhodochytrium spilanthidis* Lagerh. (after Lagerheim); F, part of a branched thread; G, swarmer; H, resting cell.

The Colonial Chlorococcales

In the preceding matter a number of the principal unicellular members of Chlorococcales have been described. Many genera of this order are, however, colonial forms and most of these appear to be azoosporic, although a discovery of motile reproductive stages in the one or the other would not be surprising. Their classification presents certain difficulties and no two authorities are in agreement as to the underlying principles to be chosen. Since a natural classification is scarcely possible in the present state of our knowledge, it is easiest to group these forms in accordance with the type of colony produced, so that the following consideration in the main epitomises the principal types of colony-structure found among the Chlorococcales.

Chlorellaceae. *Radiococcus* (186) is a colonial member of the Chlorellaceae (comprising *Chlorella*, *Micractinium*, *Trochiscia*, etc.), in which four tetrahedrally arranged chlorococcoid cells are enveloped in a wide spherical mucilage-envelope which occasionally shows a radiate structure (fig. 44 A); the cells are globose or, just after division, angular as the result of mutual pressure. Reproduction is effected by the formation of four-celled colonies within each cell of the parent, after which the membrane breaks into a number of pieces (fig. 44 B), the remnants persisting for some time at the periphery of the new group. Several such daughter-colonies may be found enclosed within a wider mucilage-envelope (fig. 44 B), but it appears that they ordinarily become free soon after their formation, since four-celled colonies are much the commonest.

Oocystaceae. *Oocystis*, the type genus of the Oocystaceae, has many species which occur singly, but a number are colonial. The cells are most usually oval or ellipsoidal with rounded or pointed ends and possess a firm membrane which is often provided with an internal thickening at each pole (fig. 44 C). The chloroplasts are always parietal and there are usually several; they take the form of discs or stellately lobed plates and the former are in most cases devoid of pyrenoids. Reproduction is effected by the division of the cell-contents into 2–8 autospores, these usually becoming free soon after their formation. In some species (e.g. *O. lacustris* Chod. (35), *O. panduriformis* West, fig. 44 D), however, they remain enclosed in small groups within the gelatinised membrane of the parent-cell, whilst in others, like *O. gloeocystiformis* Borge (fig. 44 E), several successive generations may be enclosed in this way in a common envelope.

The majority of the species of *Oocystis* are freshwater plankton forms, although a few occur in brackish water. The allied genera *Franceia*, *Lagerheimia*, and *Chodatella* are in the main non-colonial and show greater specialisation to the planktonic mode of life in the fact that the membrane is produced into a number of bristles. In *Franceia* (125) these are numerous and evenly thin throughout their length (fig. 44 F), whilst in *Chodatella* (125, 218) they taper from the base to the apex and are commonly limited in number. In *Lagerheimia* (34, 219) there are always four, more or less symmetrically disposed bristles which exhibit a wart-like thickening at the base (fig. 44 I). Many systematists include *Chodatella* in *Lagerheimia*.

It is of interest that Wille (227) has recorded the occurrence of *Tetraëdron*-like stages (fig. 44 H) in the life-cycle of *O. submarina* Lagerh.; after a period of rest the contents divide to form a number of the typical cells of the species (fig. 44 G).

A rather more specialised form than *Oocystis* is represented by *Nephrocytium* (35, 144), where the cells are usually rather elongate and commonly curved, being sometimes almost reniform (fig. 44 K); there are no polar thickenings. The chloroplast is a large curved parietal plate with a pyrenoid. The cells to the number of 2–16 are placed peripherally within a well-defined mucilage-envelope which is derived from the membrane of the parent (fig. 44 K). In *N. ecdysiscepanum* West (222 a) the membranes of dividing individuals become thick and stratified, the outer layers remaining firm and sooner or later splitting open on one side, whilst the inner ones become highly gelatinous and enclose the daughter-individuals. When these in their turn divide, the same thing happens and thus fan-shaped aggregates of some size arise which display the firmer layers of the successive membranes more or less fitting into one another (fig. 45 A). The method of colony-formation shows analogies with that characteristic of the Dictyosphaeriaceae (p. 163) and there are also resemblances to some of the Chlorodendrineae (*Ecballocystis*).

A peculiar form, probably related to the Oocystaceae, is *Gloeotaenium Loitlesbergerianum* Hansg.[1] which occurs occasionally in moorland waters. The ellipsoidal or globose cells are found singly or in twos or fours (rarely eight) within a thick stratified mucilage-envelope and are separated from one another by mucilage (fig. 45 B–D). When four cells are present they are arranged in one plane or more rarely tetrahedrally. The single-celled colonies arise by fission of the two-celled ones ((92) p. 423). The chloroplast is a parietal plate with a pyrenoid.

The characteristic feature lies in the presence, within the outermost layers of the envelope, of bands of doubly refractive calcite which appear grey or almost black. These bands are deposited along the lines of division of the cells, being transverse in the two-celled (fig. 45 B, D), but more or less cruciately arranged in the four-celled colonies (fig. 45 C). In addition there are polar (*p*) and, in the four-celled colonies, equatorial caps (*e*) of calcite deposited in slit-shaped spaces within the envelope. According to Transeau (208) reproduction is effected by a

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[1] See (84), (92), (199), (200), (208). There is some doubt, in view of the different appearance of the side-view, whether the forms studied by Transeau and by Huber-Pestalozzi may not belong to distinct species.

great increase in the size of the cells, accompanied by disappearance of the envelope except for the bands which hold the cells together for a period. When the latter are liberated they have thick or thin membranes, the former type constituting resting cells. Division of the cells to form daughter-colonies may, however, also occur whilst still enclosed in the envelope of the parent-colony ((92) p. 463).

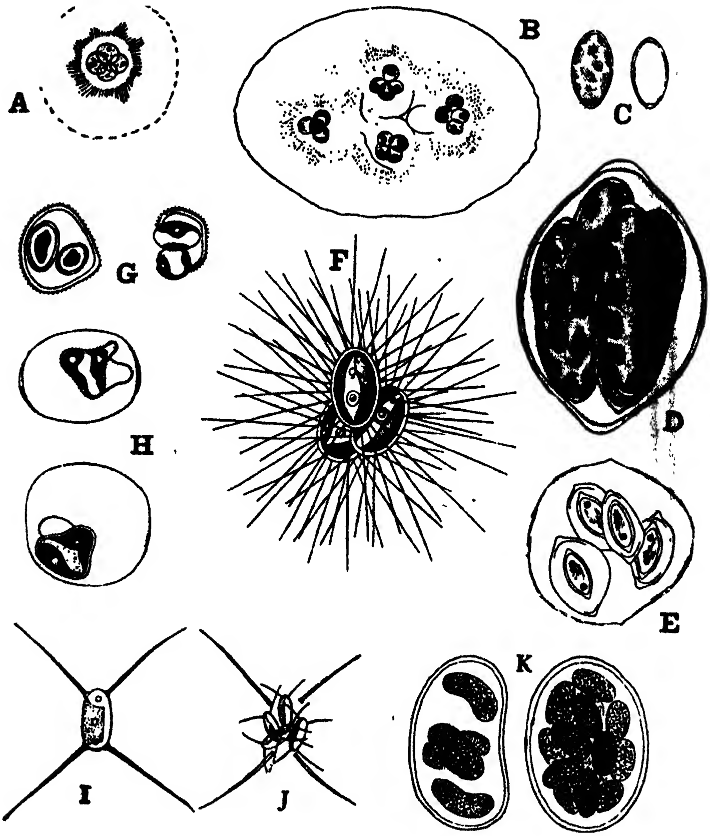

Fig. 44. A, B, *Radiococcus nimbatus* (De Wild.) Schmidle (after De Wildeman). C, *Oocystis solitaria* Wittr., and D, *O. panduriformis* West (both after West). E, *O. gloeocystiformis* Borge (after Borge). F, *Franceia ovalis* (Francé) Lemm. (after Francé). G, H, *Oocystis submarina* Lagerh. (after Wille); G, germination of and H, formation of *Tetraëdron*-stages. I, J, *Lagerheimia ciliata* (Lagerh.) Chod. (after Chodat); J, liberation of autospores. K, *Nephrocytium Agardhianum* Naeg. (after Naegeli).

The Oocystaceae may be said to exhibit one of the simplest possible methods of colony-formation in that the cells are held together merely by the gelatinisation of the membranes of the parents. A greater degree of specialisation is perhaps to be presumed in those cases in which there is a localised secretion of mucilage to hold the individuals together, as in a number of forms that are conveniently classed as the Selenastraceae ((221) p. 127). The wide envelopes of general mucilage to be found in some of these forms (as also in *Radiococcus*) are probably in the main to be regarded as an adaptation to the planktonic mode of life (cf. (146)).

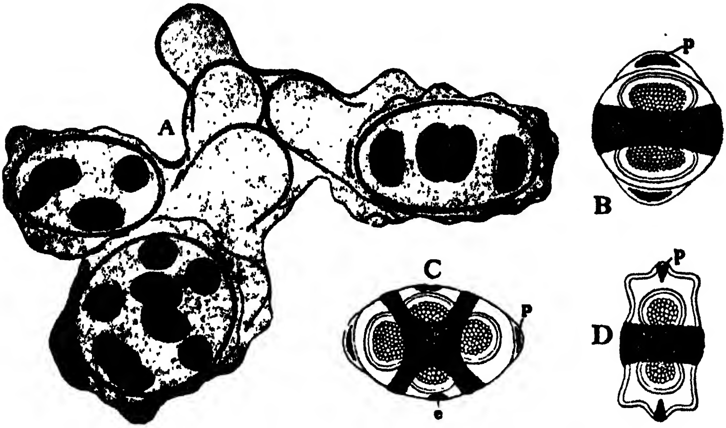

Fig. 45. A, *Nephrocytium ecdysiscepanum* West (after West), compound colony. B–D, *Gloeotaenium Loitlesbergerianum* Hansg. (after Stockmayer); C, a four-celled colony; D, two-celled colony seen from the side. *e*, equatorial, and *p*, polar caps of calcite.

Selenastraceae. In a number of these forms the loose colonies are merely produced by the cells cohering at some point of their surface, as in *Dactylococcus* (39, 144) (fig. 46 D),[1] *Selenastrum*, and *Ankistrodesmus* (*Rhaphidium*). The figures will illustrate the essential features without a lengthy description. There can be little doubt that cohesion in these forms is due to local developments of mucilage, although these are usually difficult to detect. In *Selenastrum* (fig. 46 A) the lunate cells are apposed by their convex surfaces. *Kirchneriella* (33, 184, 218), common in the plankton of lakes, is very similar, but here the cells are aggregated in one or more groups within a wide mucilage-envelope (fig. 46 B).

The needle-shaped cells of *Ankistrodesmus* are to be found singly

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[1] Cf. p. 176. Some authorities (228) have doubted the independence of this genus.

or in bundles in all kinds of freshwaters.[1] The cells possess a single parietal chloroplast occupying the greater part of the length of the cell and with or without pyrenoids (fig. 46 E). The daughter-individuals (autospores) are formed by two successive transverse divisions of the protoplast (cf. also fig. 46 C of *Kirchneriella*), preceded by division of the nucleus into four ((148) p. 63), the products growing past one another till they assume a parallel arrangement (fig. 46 F). The division is often described as oblique, but this is probably based on observation of the accomplished process, when the new protoplasts are commencing to elongate. In some species there is also crosswise division into four or longitudinal division ((148) p. 65). The autospores are liberated by gelatinisation or rupture of the membrane of the parent.

In *Ankistrodesmus falcatus* var. *stipitatus*, an attached form, the membrane of the parent-cell opens at one end, and the daughter-cells often become fixed at the aperture as a radiating tuft (fig. 46 G). If this is repeated characteristic dendroid colonies arise (37, 213). *Actidesmium* (135, 179, 197),[2] reproducing by zoospores, forms colonies in the same way. The biflagellate swarmers produced by successive division of the spindle-shaped cells, pass out of the gelatinised apex of the latter (fig. 46 H, L) and settle down there to form a radiating group of new individuals (fig. 46 I). Similar colonies are found in *Actinastrum* (33, 120). Division of the cells is crosswise, usually into eight parts, which are set free by rupture of the parent-wall, but cohere by mucilage at their proximal ends to form small radiating groups. As a result of repeated division colonies of some size are sometimes formed (fig. 46 J).

Quadrigula (169) differs from *Ankistrodesmus* essentially only in the formation of new individuals by two simultaneous longitudinal divisions in planes at right angles to one another, the cells remaining embedded in regular groups of four in the delicate mucilage produced by the gelatinisation of the parent-membrane. Colonies comprising several generations (fig. 46 K) are often held together in a common mass of mucilage (cf. *Radiococcus*).

Dictyosphaeriaceae. Under this name one can group a number of colonial Chlorococcales in which the cells are joined together by the empty parent-cell membranes, although enveloping mucilage is often present as well. *Dictyosphaerium*,[3] a common freshwater planktont, has approximately spherical or ellipsoidal colonies (fig. 47 A), although larger ones may be of more irregular shape. The cells, which show

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[1] A species of the genus has been described as the cause of green snow in the Tatra mountains (82), but according to Vischer ((214a) p. 82) this is really a *Raphidonema* (p. 262).

[2] Printz ((171) p. 94) suspects this genus of belonging to the Xanthophyceae.

[3] See 6), (144), (187), (198), (232).

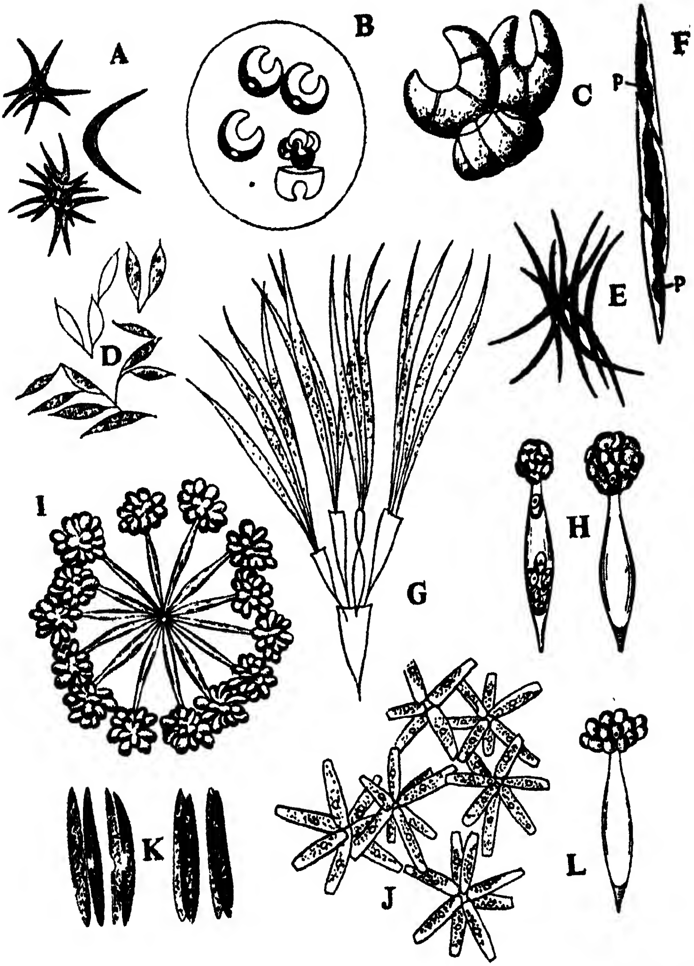

Fig. 46. A, *Selenastrum Westii* Fritsch. B, C, *Kirchneriella lunaris* (Kirchn.) Moeb.; C, dividing cells. D, *Dactylococcus bicaudatus* A. Br. var. *subramosus* West. E, *Ankistrodesmus falcatus* (Corda) Ralfs. F, *A. falcatus* var. *acicularis* A. Br., division. G, *A. falcatus* var. *stipitatus* (Chod.) Lemm. H, I, L, *Actidesmium Hookeri* Reinsch; H, L, liberation of daughter-individuals. J, *Actinastrum Hantzschii* Lagerh. K, *Quadrigula closterioides* (Bohlin) Printz. *p*, pyrenoid. (B, C, G after Chodat; H, I, L after Miller from Printz; J after G. M. Smith; K after Printz; the rest after West.)

chlorococcoid structure, are disposed near the periphery and are connected together by a system of forked threads (fig. 47 A, *t*), radiating out from the centre and representing the remains of the successive parent-cell membranes. The four (rarely two) individuals, resulting from the division of the protoplast of the parent-cell (fig. 47 B), remain adhering to the tips of the four lobes (fig. 47 C and D, *t*) into which the membrane splits and which subsequently roll up to form threads. Since this occurs in several successive generations, colonies composed of many four-celled groups result. There is an extensive mucilage-envelope showing numerous fine

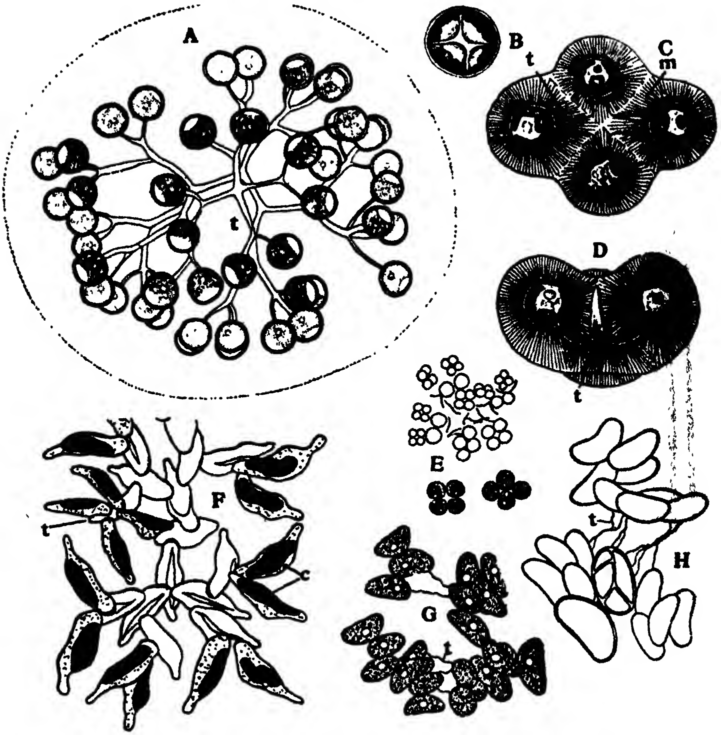

Fig. 47. A–D, *Dictyosphaerium pulchellum* Wood; B, cell-division; C, four-celled colony from above, and D, from the side. E, *Westella botryoides* Wildem. F, *Dichotomococcus capitatus* Korschik. G, H, *Dimorphococcus lunatus* A. Br. *c*, chloroplast; *m*, mucilage; *t*, connecting threads formed from mother-cell membranes. (A after G. M. Smith; B–D after Senn; F after Korschikoff; the rest after West.)

radial striations (fig. 47 C, D), but generally only visible after staining. Multiplication is apparently in the main effected by dissociation of the colonies. Biflagellate zoospores have been recorded (134), but this, though in no way improbable, requires confirmation.[1] *Westella* (*Tetracoccus* (190, 222)) is chiefly distinguished by the cells being disposed in one plane (fig. 47 E).

In Korschikoff's *Dichotomococcus* (111) the membranes of the parent-cells merely develop a longitudinal split, through which the daughter-cells (usually two) emerge, to remain clinging to its edges (fig. 47 F).

Very similar to *Dictyosphaerium* is the likewise planktonic *Dimorphococcus* (13, 56), which is apparently commoner in tropical waters. The mode of colony-formation is the same (fig. 47 G), although there is often little or no enveloping mucilage. The four individuals arising from a parent-cell are disposed obliquely in one plane and are dimorphic, the two central ones of each group being ellipsoidal or oblong, while the two outer ones are cordate or reniform (fig. 47 H). The only method of reproduction known is by fragmentation.

The colonies of the Dictyosphaeriaceae and of several of the other forms previously considered may be regarded as being composed of a number of coenobia (being compound coenobia or syncoenobia), since any individual cell gives rise to a new group whose members do not divide until a fresh phase of multiplication sets in. Coenobia of a more definite stamp are, however, characteristic of the Hydrodictyaceae and Coelastraceae, which probably represent the most highly evolved types among the colonial Chlorococcales and are no doubt closely allied, although in Brunnthaler's system (28) of classification they are referred respectively to the Zoosporinae and the Autosporinae. In the present state of our knowledge it is not easy to draw a sharp line between them. Moreover, it is possible that they may be more nearly allied to the coenobial Volvocales than to the simpler members of the Chlorococcales. Both here and there we have the apposition of what are essentially zoospores to form daughter-coenobia, although in the Volvocales the flagella are retained, whereas here they are lost. Both in the Volvocales and the Hydrodictyaceae too there is a liberation of independent swarmers in sexual reproduction.

THE FAMILY HYDRODICTYACEAE

To this family are referred *Euastropsis*, *Pediastrum*, *Sorastrum*, and *Hydrodictyon*.[2] The coenobia of the first-named (121) are composed

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[1] Zopf ((232) p. 20) states that, according to Kirchner (103) also, there is swarmer-formation in *Dictyosphaerium*, but I have been unable to find any mention of this in Kirchner's work.

[2] Probst (173) suggests that *Tetraëdron* should also be included in this family as its simplest representative. This is plausible, but must await the verification of the occurrence of zoospores.

of two flattened cells, joined along their straight inner margins, while the outer margins are widely notched, so that they present a superficial resemblance to an *Euastrum* (fig. 48 A). The chloroplast is parietal with a single pyrenoid (*p*). Reproduction is effected by successive division of the protoplast to form 2–32 biflagellate zoospores, which are liberated into a mucilage-vesicle through a tear in the parent-membrane (fig. 48 B). Within the vesicle they show a slight degree of movement, but soon round off and become arranged in pairs to form a number of new coenobia (fig. 48 C). The usual development of several coenobia from one parent-cell is really the only marked distinction from *Pediastrum*, although even in the latter an occasional formation of two or more coenobia from one parent-cell has been recorded ((53) p. 5, (173)).

The disc-shaped coenobia of *Pediastrum* are abundant in freshwater plankton, and also occur commonly in ponds and ditches amongst other water-plants. The cells are arranged in a single layer (rarely double in the middle of large coenobia) and either have almost plane faces, so that they fit closely together (fig. 48 H), or are more or less extensively lobed (fig. 48 E), so that spaces of variable size occur between them. The marginal cells mostly differ in shape from the others and are generally produced on their outer surfaces into a pair of diverging processes, although a few species have only a single process. The number of cells is usually some multiple of two and they are commonly arranged in distinct rings around a central one,[1] although these arrangements are sometimes departed from (cf. (19), (86), (88), 190)).

The smallest coenobia are found in *P. tetras* (fig. 48 I), where they are four- or eight-celled, while those of the common *P. Boryanum* (fig. 48 H) sometimes comprise 128 cells. The chloroplast takes the form of a parietal plate, often showing some perforation, and contains 1–4 pyrenoids; the older cells have several nuclei. Petersen (160, 161) has recorded the presence of tufts of rigid gelatinous bristles on the apices of the processes of the marginal cells (fig. 48 G) and sometimes also on the surfaces of the central ones; they are no doubt an additional equipment for planktonic life, and in this connection it is of interest that in some species they have been found to disappear in winter.

Asexual reproduction (19, 87, 194) takes place by means of biflagellate zoospores, formed by successive nuclear division followed by progressive cleavage of the protoplast. The swarmers are suddenly liberated through a slit in the wall (fig. 48 H) into an external vesicle

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[1] In an 8-celled coenobium, 1 + 7; in a 16-celled one, 1 + 5 + 10; in a 32-celled one, 1 + 5 + 10 + 16. These groupings represent the most compact arrangement possible.

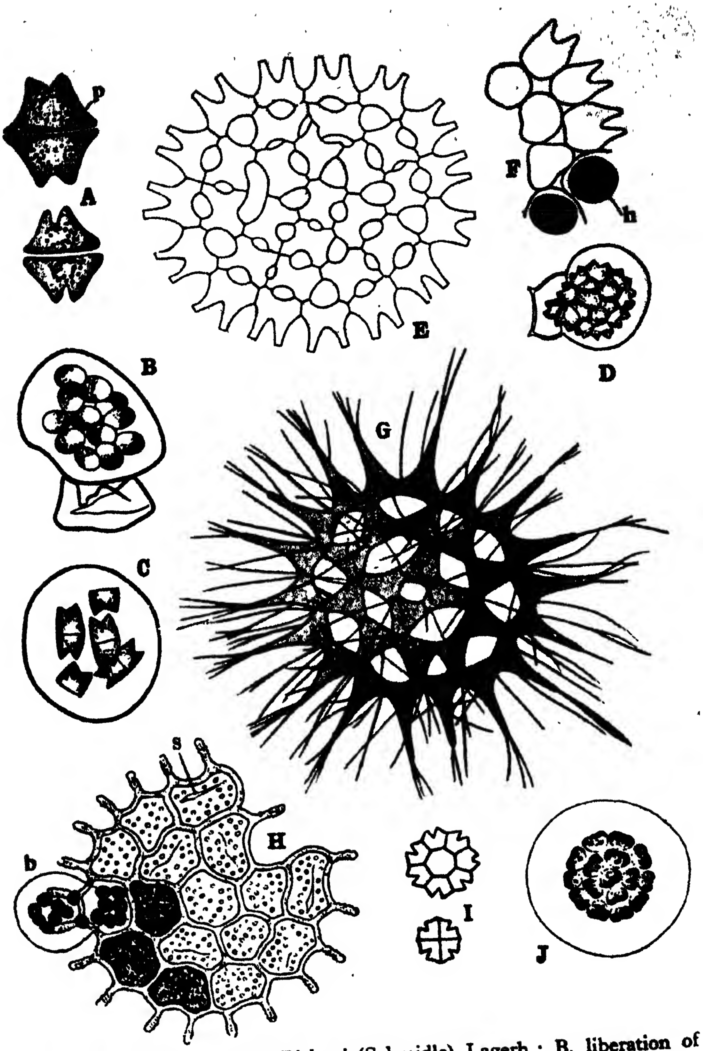

Fig. 48. A–C, *Euastropsis Richteri* (Schmidle) Lagerh.; B, liberation of swarmers; C, formation of daughter-coenobia. D–J, *Pediastrum*. D, *P. Boryanum* (Turp.) Menegh., germination of polyhedron. E, *P. duplex* Meyen var. *clathratum*. F, *P. duplex*, with hypnospores (*h*). G, *P. clathratum* (Schröt.) Lemm., mucilage-bristles. H, J, *P. Boryanum* var. *granulatum*; H, formation and liberation of zoospores; J, formation of new plate. I *P. tetras* (Ehrenb.) Ralfs. *b*, bladder of mucilage; *p*, pyrenoid; *s*, slit in wall (A–C after Lagerheim; D after Askenasy; E after G. M. Smith; F, I afte West; G after Petersen; H, J after Braun.)

(*b*)[1] within which they exhibit active movements in all directions. Gradually they assume a more orderly arrangement and become disposed in one plane to form a new coenobium which acquires its mature characteristics before liberation from the vesicle (fig. 48 J). According to Harper ((87) p. 392; (88) p. 238) the peripheral series comes to rest before the inner ones. Complete suppression of flagella and of all movement is apparently not uncommon ((220) p. 217), in which case *Pediastrum* behaves exactly like one of the Coelastraceae (cf. p. 174). Probst (173) records cases in which four new coenobia are formed from a parent-cell (cf. with *Sorastrum* below). Formation of one or more hypnospores (fig. 48 F, *h*) from the cell-contents occasionally takes place (53, 201). The sexual reproduction is dealt with below.

We owe a detailed study of the formation of the colony in *Pediastrum* to Harper ((87), (88); cf. also (89), (140), (212)). The cells of the commonly occurring species are usually two-lobed, but this inherited form in most cases attains its full expression only in the peripheral series of cells which have the largest proportion of free surface; in those of the inner series the influence of internal environment in modifying the inherited form is clearly illustrated. Only in a few species, like *P. clathratum* (Schröt.) Lemm., do the inner cells attain the same form as the outer ones (fig. 48 G).

In *Sorastrum* ((13) p. 40, (144) p. 98, (181)) the coenobia are approximately spherical and composed usually of 16–64 cells which are wedge-shaped, sublunate, or reniform (fig. 49 A, F). The broad surfaces of the cells bear a number of spines and are directed outwards, while the inner extremities are produced into colourless cellulose stalks whose ends are united in the centre to form a small facetted sphere (fig. 49 A, B). The young cells possess a curved plate-shaped chloroplast with a pyrenoid apposed to the outer wall, but in older cells the chloroplast covers most of the inner surface of the wall, although no increase of pyrenoids normally takes place. The mature cells are multinucleate.

The accounts of zoospore-formation differ appreciably. Probst (172, 173) states that the cell-contents of *S. spinulosum* divide successively into 8–64 parts which are liberated into the usual vesicle. Each of these gives rise to 4–32 zoospores, each group, even during the limited period of movement, remaining distinct from its neighbours and ultimately organising a distinct coenobium. The alga would thus resemble *Euastropsis* in forming several new colonies from one parent-cell. Geitler (72), however, for the same species describes

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[1] According to Probst (173) this vesicle, both here and in *Sorastrum*, is formed by swelling of the inner pectic layers of the cell-membrane which thus burst open the outer ones.

a successive division of the chloroplast into as many parts as the future number of zoospores (fig. 49 C), and a subsequent progressive cleavage of the protoplast after the manner recorded for other Hydrodictyaceae (fig. 49 D). Moreover, it appears that he never observed the formation of more than one coenobium from a mother-cell. In the production of the new coenobium the biflagellate swarmers become grouped with their apices facing inwards (fig. 49 E) and, after secreting membranes, the inner ends grow out into the cellulose stalks. *Sorastrum* might be regarded as a colonial *Characium* in which the

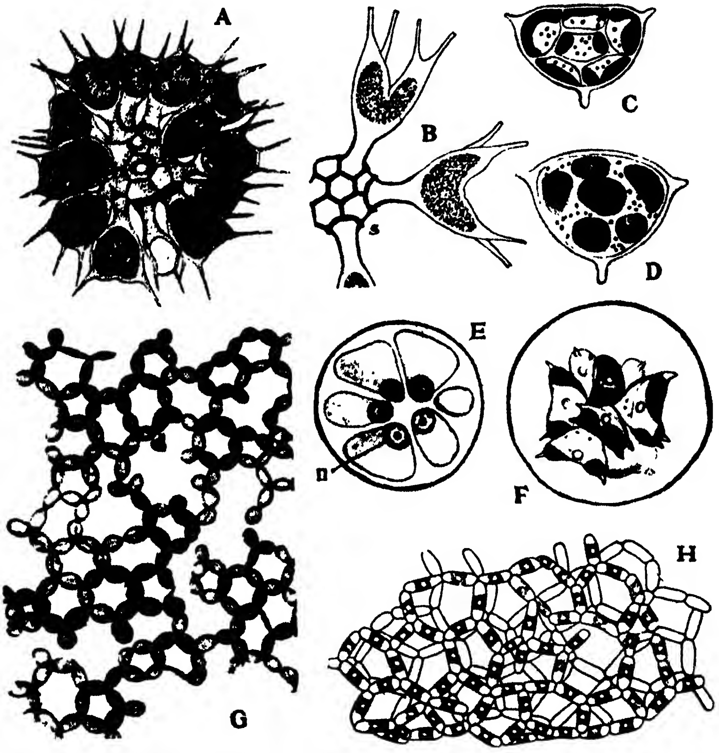

Fig. 49. A–F, *Sorastrum*. A, B, *S. americanum* (Bohl.) Schmidle (A after Bohlin; B after Schröder); B shows the stalks of the cells and the central sphere (*s*) formed by their inner ends. C–F, *S. spinulosum* Naeg. (after Geitler); C, D, development of zoospores; E, F, young coenobia within vesicle, in E pyrenoids not yet differentiated. G, *Hydrodictyon africanum* Yaman. (original photo). H, *H. reticulatum* (L.) Lagerh. (after G. M. Smith). *n*, nucleus.

stalks of the individuals are attached to one another, instead of to a substratum.

Hydrodictyon reticulatum, the water-net, is a rare alga which, however, occasionally occurs in prodigious quantities. The coenobium in this case is a free-floating hollow cylindrical network (fig. 49 H), closed at either end, and reaching a length of as much as 20 cm.[1] The meshes of the net are pentagonal or more usually hexagonal, the angles being formed by the union of three of the elongate multinucleate cells (fig. 50 A). The latter are cylindrical and have a large central vacuole, the lining layer of cytoplasm containing the nuclei and a complex reticulate chloroplast (106) with numerous pyrenoids (fig. 50 B). The cells of young coenobia, according to Lowe and Lloyd (130), possess a simple chloroplast in the shape of an incomplete parietal band (cf. fig. 49 H) which, with the lengthening of the cells, takes on a spiral form. The spiral later branches and gradually more and more numerous fenestrations appear which ultimately, according to these observers, lead to the division of the chloroplast into numerous small reticulately arranged portions, some of which contain pyrenoids.

Similar steps are described by Wigglesworth (224) in the case of *H. africanum* (230), but there is no evidence to show that the mature chloroplast is here anything but a complex reticulum. The species just mentioned forms saucer-shaped coenobia, circular in form and often somewhat turned up at the edges. The young cells are again cylindrical, but later become ellipsoidal (fig. 49 G) and ultimately swell up to form huge spheres, 1 cm. or more in diameter, which fall apart from one another and lie like numerous green marbles on the bottom of the shallow waters which this species frequents. It appears that these huge coenocytes ultimately produce gametes.[2] Wigglesworth found no evidence of asexual reproduction, but it can hardly be doubted that new nets are formed from the ordinary segments of the coenobium, as in *H. reticulatum*.

Here asexual reproduction takes place in the following way.[3] Many thousands of uninucleate, biflagellate zoospores are formed by progressive cleavage of the protoplasm of the mature coenocytes into smaller and smaller fragments (fig. 50 E, F). They remain confined within the membrane of the parent coenocyte, exhibiting the usual restricted movements, and ultimately withdraw their flagella, secrete membranes and become arranged to form a new net (fig. 50 C, D). According to Klebs (107) the zoospores are permanently connected by short threads, but subsequent workers (99, 130) have been unable to

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[1] Iyengar's *H. indicum* (93) is a larger form with bigger cells and meshes and thick lamellated walls.

[2] The statement on p. 117 of *British Freshwater Algae* (221) that they form new coenobia is erroneous.

[3] See (2), (55), (106–108), (150), (205).

confirm this. The necessary space for the movement of the swarmers is created by the swelling of the longitudinal walls and a reduction in the size of the vacuole ((99) p. 61). When the zoospores first come to rest, they show a distinct tendency to become arranged in straight rows in three directions, at angles of 60° to one another, although, as

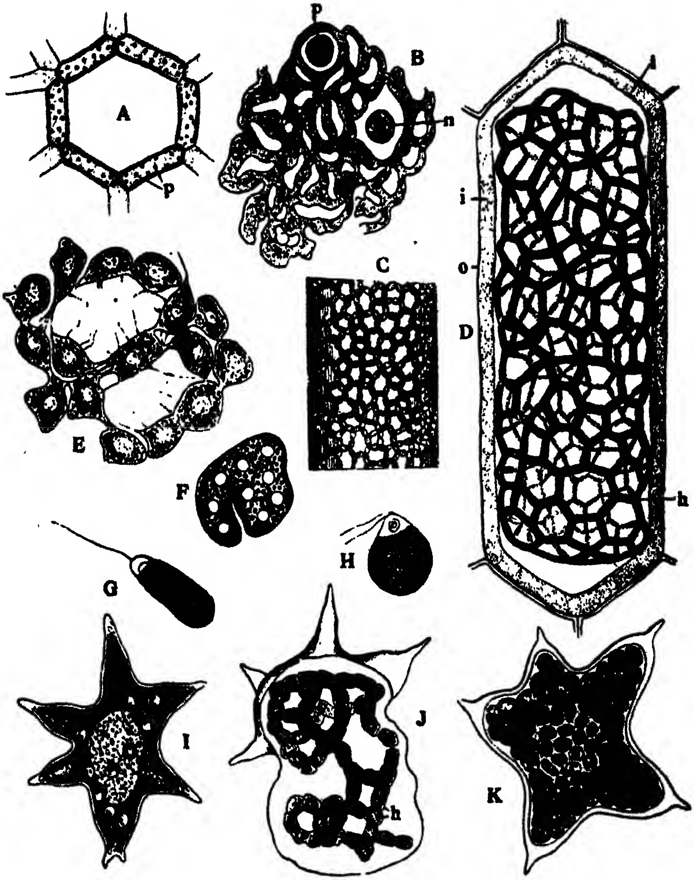

Fig. 50. Structure and reproduction of *Hydrodictyon reticulatum* (L.) Lagerh. A, group of cells; B, part of chloroplast; C, D, formation of new nets; E, F, small parts of protoplast showing fission to form zoospores, E a later stage than F; G, H, swarmers from the zygospore; I, polyhedron-stage; J, net-formation within same; K, swarmer-formation in polyhedron. *h*, young nets; *i*, inner layer of wall; *n*, nucleus; *o*, outer layer of wall; *p*, pyrenoid. (C after Harper from Oltmanns; G–K after Pringsheim; the rest after Klebs.)

the cells begin to enlarge, this arrangement becomes obscured. This grouping is that which, on theoretical grounds, allows of the largest number of cells in the smallest area and yet admits of the formation of a network with hexagonal meshes (85, 130). The hexagonal mesh is the most economical of material and at the same time affords the greatest strength and elasticity (cf. also (99)).

Sexual reproduction has so far only been observed in *Pediastrum* (9, 19) and *Hydrodictyon* (2, 107, 108, 133, 168). The biflagellate isogametes are produced in the same way as the zoospores, but are formed in larger numbers and are consequently smaller; they are, moreover, liberated as individual swarmers through a hole in the parent-cell membrane. *Hydrodictyon* is monoecious and even gametes from the same coenocyte may copulate. The flagella are withdrawn immediately after fusion and a spherical zygote with a thin membrane is formed. This gradually enlarges during the ensuing period and stores oil which is coloured red by haematochrome. Ultimately these zygospores undergo two successive divisions to form four large biflagellate swarmers (fig. 50 G, H), during which reduction probably occurs (133). The swarmers contain numerous discoid chloroplasts without pyrenoids and, on coming to rest, develop into polyhedral cells (fig. 50 I) which closely resemble some species of *Tetraëdron* (168) and continue to enlarge for some time. Aplanospores developing directly into polyhedra have also been observed. Ultimately the polyhedra undergo division of their contents to form zoospores (fig. 50 K) which combine to form a new net in the manner already described. The young, relatively few-celled net is spread out in one plane and is set free by rupture of the outer layers of the polyhedral cell (fig. 50 J), although remaining for a time enclosed within the dilated inner layers. In the case of *Pediastrum* the formation of swarmers from the zygospores and their development into polyhedra has recently been observed by Palik (151), while Askenasy (9) showed that new plates develop within the polyhedral cells (fig. 48 D).

The huge coenocytes of *Hydrodictyon africanum* above mentioned produce numerous biflagellate swarmers, some of which have been observed to escape into the water. There is every probability that they represent gametes and that they give rise, with or without fusion, to spherical, orange-coloured resting spores. These appear to form the new nets directly, without the intervention of polyhedral stages (224), but Mainx (133) suggests that the spores observed are germinating parthenospores and not zygotes. In any case further observations are necessary to establish that this species has a life-history differing from that of *H. reticulatum*, where the usual swarmers formed by the reduction division delay net-production until they have passed through a prolonged resting period accompanied by growth.

THE FAMILY COELASTRACEAE

Chodat's *Fernandinella* ((42) p. 102) is an incompletely known form which Petersen ((161*a*) p. 34) has found also in soils. It has few-celled coenobia reproducing by the formation of quadriflagellate zoospores, but in Chodat's material multiplication by the formation of new coenobia within the cells of the parent was the rule. Its affinities are unclear, but in its capacity to form swarmers, as well as to produce new coenobia, it recalls the occasional suppression of flagella in the zoospores of *Pediastrum* and indicates a trend in the direction of the Coelastraceae. The peculiar genus *Marthea* described by Pascher(154) affords another connecting link. Here four spindle-shaped cells, possessing a curved parietal chloroplast with an indistinct pyrenoid, are grouped at right angles to one another in a single plane (fig. 51 A), their inner ends being embedded in a central mass of mucilage. New coenobia are formed by division of the protoplast into four elongate amoeboid cells, lacking flagella but provided with contractile vacuoles and stigma. The amoeboid movements soon cease and the four individuals become arranged in the characteristic cruciate fashion, secreting at their inner ends a small stalk which swells and gradually coalesces with the others to form the central mucilaginous mass. The new coenobia may remain for a time enclosed within the membrane of the parent-cell forming small syncoenobia (fig. 51 A).

In the typical Coelastraceae the cells of the coenobia are in most cases joined together by mucilage-pads or by processes of other kinds developed at certain points of the surface from the thin envelope of mucilage which surrounds the firmer part of the wall(187). In addition there is sometimes a common mucilage-investment around the whole coenobium, although rarely visible without special staining (fig. 51 F). There is always a single parietal chloroplast, usually with a pyrenoid. In *Crucigenia* (including *Staurogenia*)(185, 225) the coenobia are formed of four cells of diverse shape arranged to form a flat or slightly curved plate, the cells being closely adherent except in the centre, where there is usually a quadrate or rhomboidal space (fig. 51 B). The daughter-coenobia, formed by crosswise division of the protoplasts of the parent, are generally combined to form larger plates, which are held together by a more or less conspicuous mucilage-envelope. In *Hofmania*(36) the ruptured fragments of the parent-cell membranes persist for a time around the new coenobia (fig. 51 F).

The numerous species of *Scenedesmus*[1] possess four- or eight-celled (rarely 16-celled) coenobia, composed of ellipsoid, oblong or fusiform cells, usually grouped in one plane with the long axes of the cells parallel to one another (fig. 51 D, E, M); the cells sometimes lie in

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[1] See (47), (79), (187), (190), (192).

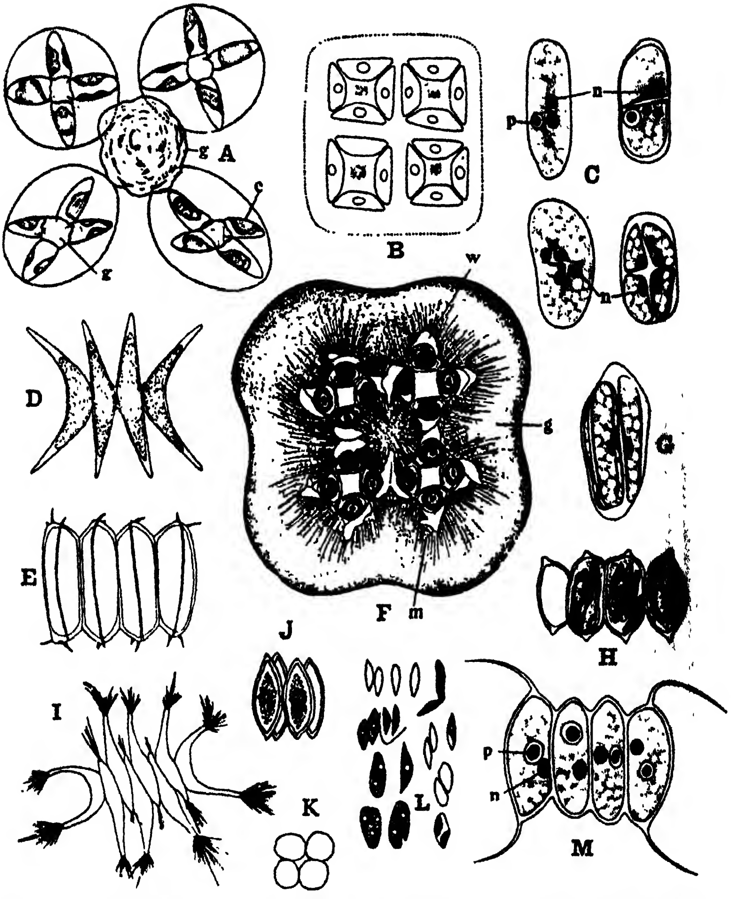

Fig. 51. Coelastraceae. A, *Marthea tetras* Pascher. B, *Crucigenia Tetrapedia* (Kirchn.) West. C, G, H, M, *Scenedesmus quadricauda* (Turp.) Bréb.; C, four successive stages in formation of daughter-coenobium; G, the latter still within the membrane of the parent-cell; H, reproducing coenobium; M, mature coenobium. D, I, *Scenedesmus acuminatus* (Lagerh.) Chod.; I shows mucilage-bristles. E, *S. brasiliensis* Bohlin. F, *Hofmania Lauterborni* (Schmidle) Wille. J, K, *Tetradesmus cumbricus* West; K, end-view. L, *Dactylococcus*-stage of *Scenedesmus obliquus* (Turp.) Kütz. *c*, chloroplast; *g*, *m*, mucilage; *n*, nucleus; *p*, pyrenoid; *w*, remains of cell-membranes. (A after Pascher; B after Schmidle; C, G, M after Smith; D after Fritsch; E after Deflandre; F after Oltmanns; H after Senn; I after Petersen; the rest after West.)

two alternating rows. The terminal cells of the row commonly differ in shape and ornamentation from the others. A reference to the figures will illustrate the diversity of cell-shape and ornamentation. In the few species which have been fully studied it has been found that the ornamentations (e.g. the large spines of *S. quadricauda* (Turp.) Bréb., fig. 51 M), as well as the connecting pads between the cells, are merely elaborations of the mucilage-envelope of the latter(187). The parietal chloroplast often occupies the whole length of the cell and generally possesses a single pyrenoid. The cells occasionally bear tufts of gelatinous bristles (fig. 51 I), as in *Pediastrum*(160).

Reproduction is accomplished by crosswise division of the protoplasts which takes place successively(191) (fig. 51 C) and, after the necessary adjustments, the fully developed coenobia (fig. 51 G, H) are liberated by rupture or gelatinisation of the parent-membrane. Syncoenobia are rare. Smith's *Tetradesmus*(189) only differs from *Scenedesmus* in the mode of grouping of the four cells (cf. fig. 51 J, K).

The species of *Coelastrum*[1] possess hollow spherical or polyhedral coenobia (fig. 52 A and D), composed of 8, 16, or 32 (rarely 64) cells disposed in a single peripheral layer, the whole surrounded by an indistinct mucilage-investment. The cells are often globose or polyhedral and joined along their contiguous surfaces by cushions of mucilage (fig. 52 A). In other species they are produced into more or less marked processes which are joined at their apices, so that the adjacent cells are separated by narrower or wider spaces (fig. 52 D). In *C. reticulatum* (Dang.) Senn(52) the globose cells are connected by a number of long gelatinous processes, developments of the ordinary mucilage-envelope of the cell (fig. 52 B, E, F, *p*). The young coenobia in this case often remain for a relatively long time within the parent-cell membrane and, since the processes on the latter persist, syncoenobia are of common occurrence (fig. 52 E, F). In other species the daughter-coenobia are usually liberated as soon as they are fully differentiated, mostly through a split in the cell-wall (fig. 52 A, G).

Several investigators(11, 177, 187) have studied the growth of species of *Scenedesmus* and *Coelastrum* under various cultural conditions and have shown that the cells may be made to assume very diverse forms, e.g. *Dactylococcus*-like stages, *Chlorella*-like forms, etc. It is not clear, however, how far this polymorphism obtains in nature, although it is probable that *Dactylococcus infusionum* Naeg. (fig. 51 L) is a naturally occurring state of *Scenedesmus obliquus* (Turp.) Kütz. (79).[2] The reversion of the cells to a state and a method of multiplication indistinguishable from *Chlorella* (fig. 52 H), a condition which may moreover persist through several generations, is of considerable phylogenetic interest. Grossmann(81) concludes that colony-formation is favoured

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[1] See (57), (59), (167), (177), (187), (190).

[2] From this view Smith ((192), (196*a*) p. 508) dissents.

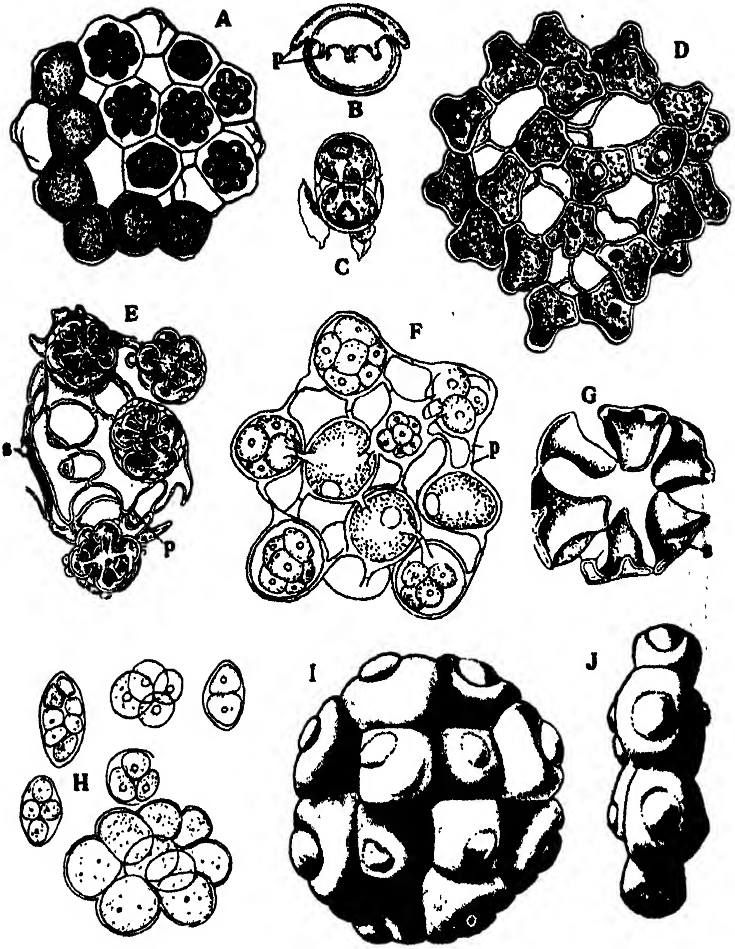

Fig. 52. A–G, *Coelastrum*. A, *C. sphaericum* Naeg. B, C, E–G, *C. reticulatum* (Dang.) Senn; B, empty cell with connecting processes; C, two-celled colony showing mode of connection of cells; E, F, formation of syncoenobia; G, remains of membranes with splits (*s*) through which daughter-coenobia have been liberated. D, *C. proboscideum* Bohlin. H, *Scenedesmus obliquus* (Turp.) Kütz., *Chlorella*-stages. I, J, *Phytomorula regularis* Kof. *p*, connecting-processes. (A after West; F, H after Chodat; I, J after Kofoid, the rest after Senn.)

by a surplus of carbohydrates, being dependent on an optimum concentration of the nutritive solution which varies at different seasons of the year.

Kofoid's *Phytomorula* (109) develops 16-celled coenobia which are like a compressed *Coelastrum*. In the centre are eight cells grouped in two layers of four, while around the periphery are eight cells symmetrically disposed in a single layer; there is no central hollow. On the outer surface of each cell lies a slightly elevated area with a narrow annular depression around its base (fig. 52 I, J). The mode of multiplication is not known.

Apart from the normal reproduction by formation of new coenobia, resting spores with a thick membrane appear occasionally to be formed in most genera of Coelastraceae (229). Chodat ((45) p. 445) has observed stages that make a formation of swarmers in *Crucigenia* probable. When it is recalled that *Sorastrum* was long regarded as an azoosporic form and referred to Coelastraceae, the possibility of other members of this family proving to have motile stages is not to be dismissed. It may in fact be questioned whether there are any longer any grounds for maintaining two families among the strictly coenobial forms. The members of the Hydrodictyaceae are already sufficiently diverse in general character to render the inclusion of the Coelastraceae in this family possible without any great alteration of the diagnosis.

THE AFFINITIES AND CLASSIFICATION OF THE CHLOROCOCCALES

This brings us back to the question of the general classification of the Chlorococcales which was raised on p. 147. If, as appears clear, the classification into zoosporic and azoosporic forms should be abandoned, it is difficult to find any other definite basis. It may even be doubted whether there is any justification in keeping the majority of the unicellular forms apart from the colonial ones. Every classification that has so far been attempted appears unnatural, because it leads to the placing of forms that are almost certainly allied in distinct families. This criticism applies equally to the system here adopted, which is frankly artificial and based on the type of colony produced.

Geitler ((72) p. 443) believes that a basis of classification can be found in the two types of division of the protoplasts to form new individuals. The one has multinucleate mature cells undergoing simultaneous division to form the new individuals (*Tetraëdron*, *Characium*, *Hydrodictyon*, *Pediastrum*, *Sorastrum*, *Coelastrum*, and possibly *Scenedesmus*). It is characteristic of this type that the pyrenoid does not divide, but persists in one of the units formed by the progressive cleavage of the protoplast (cf. fig. 51 C), sooner or later to disappear, while the daughter-cells form fresh pyrenoids. The second type is characterised by successive division of the protoplast (*Chlorococcum*, *Chlorochytrium*, *Trebouxia*, *Chlorella*, *Dictyosphaerium*), during which the pyrenoid divides, so that each daughter-cell receives one. This distinction scarcely appears to be of sufficient importance to afford an adequate taxonomic basis; moreover, there are indications that both types of division may occur in one and the same genus (cf. under *Characium* and *Sorastrum*). The cells of many forms that divide successively become multinucleate towards maturity as a preparation for the subsequent cleavage, as Geitler himself recognises, so that a sharp distinction between the two methods of division is scarcely possible.

There can be no doubt that the Volvocales and Chlorococcales are closely allied (110, 114). The frequent persistence of contractile vacuoles and sometimes of eye-spots (cf. also (159)) in the coccoid cell, even in forms that appear to have given up reproduction by swarmers, is sufficient testimony of this close relationship. To establish a special group, Vacuolatae, for such forms with contractile vacuoles, as Korschikoff ((110) p. 490) advocates, is, however, laying too much stress on a single character.

It would appear that some of the sexually reproducing Chlorococcales have become diploid, a condition noted as possibly occurring also among Volvocales (p. 119). This is highly probable for *Chlorochytrium* (p. 155) and is also likely in the case of Korschikoff's *Apiococcus* ((110) p. 474) and other forms with direct germination of the zygote. This tendency is significant in connection with the hypothesis of a possible origin of the Siphonales from this group (p. 369).

The following is an epitome of the classification followed in the preceding treatment:

1. *Chlorococcaceae:* Apiococcus, Borodinella (?), Characiochloris, Characium, Chlorochytrium, Chlorococcum, Codiolum, Dictyococcus, Hypnomonas, Phyllobium, Rhodochytrium, Tetraciella, Trebouxia.
2. *Eremosphaeraceae:* Eremosphaera.
3. *Chlorellaceae:* Borgea, Chlorella, Micractinium, Muriella, Mycotetraëdron (p. 185), Prototheca (p. 185), Radiococcus, Tetraëdron, Trochiscia.
4. *Oocystaceae:* Chodatella, Desmatractum, Franceia, Glaucocystis (p. 186), Gloeotaenium, Lagerheimia, Nephrocytium, Octogoniella, Oocystis, Scotiella.
5. *Selenastraceae:* Actidesmium (?), Actinastrum, Ankistrodesmus, Dactylococcus, Hyaloraphidium (p. 185), Kirchneriella, Quadrigula, Selenastrum.
6. *Dictyosphaeriaceae:* Dichotomococcus, Dictyosphaerium, Dimorphococcus, Westella.
7. *Hydrodictyaceae:* Euastropsis, Hydrodictyon, Pediastrum, Sorastrum.
8. *Coelastraceae:* Coelastrum, Crucigenia, Fernandinella, Hofmania, Marthea, Phytomorula, Scenedesmus, Tetradesmus.

THE ECOLOGY AND PHYSIOLOGY OF THE CHLOROCOCCALES

Many of the simpler Chlorococcales, like the Volvocales (p. 78), exhibit more or less pronounced saprophytic tendencies. *Chlorococcum humicolum* and *Chlorochytrium paradoxum* are common in cultivated soils(22, 26 139); several species of *Chlorella* thrive in organic media (sewage, etc., (11, 31)), sometimes with loss of chlorophyll (117), and others occur in the sappy exudations of trees (115). The majority of the members of this order are readily grown in artificial cultures and a large volume of literature exists dealing with the form-variations observed in such cultures and the special features of the nutrition of the diverse forms. Artari (5, 7, 8), Beijerinck (11), and especially Chodat (39) and his pupils[1] have grown a large number of Chlorococcales (*Chlorella*, *Ankistrodesmus*, *Scenedesmus*, etc.) on agar supplied solely with mineral nutriment or in mineral solutions, but they have shown that a much more luxuriant development is obtained in most cases if glucose is also present ((39) p. 87). Although many other non-nitrogenous organic compounds can be utilised (24, 209), no other form of carbohydrate appears to be as efficient as glucose, nor do organic acids in general seem to form a suitable source of organic food.

Oettli ((148) p. 35) has, however, shown that species of *Ankistrodesmus* develop well in mineral solutions containing fermenting cellulose. Many Chlorococcales (species of *Scenedesmus*, *Chlorella rubescens*, etc., cf. (39) p. 110, (203)) soften or even liquefy gelatine. The nutritive value of organic nitrogen compounds is relatively slight compared with glucose ((148) p. 40) and such compounds can be supplied in the most diverse forms (nitrates, ammonium compounds, amino-acids, peptone) to many Chlorococcales without any appreciable differences in the amount of growth, provided no other organic material is present (24, 25, 207). In media containing glucose, however, Oettli found that a full development of the colonies of *Ankistrodesmus* only took place, if nitrogen was supplied in the form of peptones. Muenscher (143) finds that *Chlorella* carries on protein-synthesis in darkness when supplied only with inorganic nitrogen.[2]

Many Chlorococcales appear to be able to produce chlorophyll in darkness (6, 7, 80, 117, 176),[3] and Dangeard (63) reports growth of *Scenedesmus acutus* for eight years in continuous darkness without loss of the green colour. On the other hand a frequent feature of algal cultures is the decolorisation (yellowing) that sets in after some time,

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[1] See (54), (79), (80), (90), (95), (148), (177), (203), (207), (213). See also the papers (62), (117), (118), (145), (209).

[2] With reference to the asserted capacity of Green Algae to fix atmospheric nitrogen, see Bristol and Page, *Ann. Appl. Biol.* 10, 378–408, 1923.

[3] This is also true of some of the Volvocales (cf. (131)).

although the cells in question are in all other respects perfectly healthy ((39) pp. 90, 118).

This decolorisation is only observed in the presence of glucose and has been ascribed to increasing deficiency of nitrogen, the phenomenon being accelerated by exposure to light. If cells of such a culture are transferred to a fresh medium with a better balance of glucose and nitrogen-compounds, normal green colonies are formed which in their turn lose their colour after some time. According to Meyer (233), however, the non-formation of chlorophyll is due to an inhibiting effect of the glucose and, as the latter gradually gets used up, the colonies become green from within outwards. *Chlorella variegata* Beijerinck (12) always develops colourless cells on agar supplied with glucose and has maintained its colourless character for thirty years in successive cultures of this type, but if transferred to agar without glucose the normal green colour reappears ((48) p. 526).

The investigation of the growth of these forms in cultures has rendered it perfectly clear that a large proportion of the Chlorococcales, while capable of a holophytic existence, possess a strong saprophytic tendency and attain a much better development under conditions of heterotrophic nutrition. This is probably equally true of many of the Volvocales (cf. p. 78). The capacity for heterotrophic nutrition must clearly exist in any alga that is to thrive beneath the surface of the soil. There is evidence that, in the case of a number of the species involved, photosynthesis alone is not adequate for luxuriant growth (27, 80, 143), but there are probably many gradations in this respect (25) between forms which in the presence of light altogether dispense with heterotrophic nutrition, and those which under all circumstances grow better in the presence of glucose. For the latter an increase in light-intensity does not directly increase the amount of glucose absorbed, but rather tends to reduce the heterotrophic in favour of autotrophic nutrition.

In the cultures of many Chlorococcales considerable diversity in the shape of the cells[1] (cf. fig. 53) and, in the case of colonial forms in the nature of the colonies, is to be observed, despite the fact that, in recent years at least, such cultures have been grown from single cells and without any admixture of foreign organisms (38, 90, 213, 214). Some of the forms thus observed appear definitely abnormal and this is possibly true of all, even of the *Chlorella*-like stages that have so often been seen in certain cultures of *Scenedesmus*, *Coelastrum*, etc. (cf. p. 176).

It may happen that in pure cultures a given alga may assume a form that is indistinguishable from that of another species or even genus, occurring in nature. It is, however, very doubtful whether this polymorphism exists in nature, and it still remains to be shown that two apparently identical forms found in different habitats are actually identical stages of two quite different Algae, found in their distinctive

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[1] Disappearance of the pyrenoid has also been observed ((117) p. 181).

forms in other habitats. Periodical studies of Algae in the same piece of water over a number of years tend to show remarkable constancy of individual species, both at different seasons and in different years. The only case that is perhaps clearly established among Chlorococcales is that of the *Dactylococcus*-stage of *Scenedesmus obliquus* (p. 176). Valuable as have been the results of pure culture work in other respects, there is little evidence that such cultures are altogether reliable for the study of the normal form-variation of algal species. It is possible, too, that in many cases a somewhat distorted picture of the life-history is obtained, since the conditions are necessarily different from those occurring in nature. As a supplement to direct observation in nature, however, the method of pure culture is invaluable.

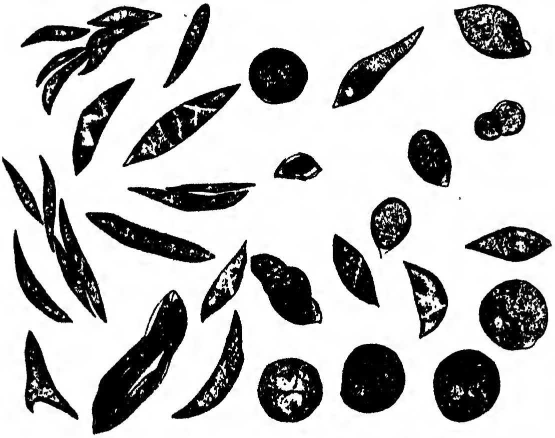

Fig. 53. *Ankistrodesmus septatus* Oettli, diverse cell-forms from a single culture (after Oettli).

An important outcome of the investigations of the Geneva school has been to establish the existence of elementary species in a large number of the genera of Chlorococcales (cf. also (5)). In many cases at least the cells of these forms are indistinguishable under the microscope ((48) p. 525), and it is not until they are grown on nutrient agar supplied with glucose (2 per cent.) that the differences become apparent in the nature of the cultural "colonies" produced.[1] That these differences are not due to variations in the media and glass vessels employed is shown by the fact that they are just as apparent when cultures of the different species are grown side by side in the same vessel. Chodat insists on the differences in question being

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[1] In media lacking glucose only slight differences are apparent. In liquid media the differences are manifested in a different rate of multiplication, as evidenced by the diverse intensity of colour of the suspensions and the different modes in the variation of cell-size ((49) p. 32).

morphological, but the form and size of cultural colony produced, the depth of colour, the production of carotin, etc. would all appear to be evidence rather of a different physiological constitution, as expressed in the rate of growth, the amount of chlorophyll formed, etc. It has been shown that the common *Chlorella vulgaris*, for instance, is represented in nature by a large number of such elementary species, as recognised in cultures on mineral agar with glucose. These species can be arranged in groups and the extremes of the different groups are often connected by a number of intermediate types.

Evidence has also been produced(49) of the origin of new elementary species by small mutations (*generalised mutation* of Chodat) in *Chlorella rubescens*, a species which, when grown on nutrient agar with glucose, develops deep red growths. Clones derived from pure cultures of this alga, that have been reinoculated without change over a long period of years, may ultimately develop a small number of new types. Chodat suggests that such micromutations give origin to elementary species and that the stability of cultures is only illusory, since new micromutations are constantly arising, although normally masked in the pure line derived from a single cell by the prevalent normal type. It remains to be seen in how far the various elementary species that have been distinguished are characteristic of definite habitats in nature.

A valuable aspect of this work is the recognition of the fact that the gonidia of *Trebouxia* (*Cystococcus*) and *Coccomyxa* (cf. p. 128), extracted from different Lichens,[1] belong to distinct races. We owe the establishment of this fact to Chodat ((39) p. 186), Waren(215), and Jaag(95, 97 *a*). The last-named has shown that even the observation of the gonidia *in situ* in the Lichen may afford evidence of more or less constant differences in form between those inhabiting different genera (*Cladonia*, *Parmelia*), and that differences are also recognisable between the gonidia inhabiting various species of the same genus. It is, moreover, of interest that the relationship of the gonidia to one another runs generally parallel with the relationships of the Lichen as implied by other characteristics(97 *a*). The differences between the gonidia also find their expression in the colonies developed from single cells on nutritive agar. These differ among one another in size (rate of growth), general conformation, and depth of colour, and these differences are constant. Jaag was unable to establish identity between the gonidia and any free-growing forms of *Trebouxia*, but he mentions the finding of a *Coccomyxa* identical with the gonidium of *Solorina saccata*(96).

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[1] The only genera of Volvocales and Chlorococcales recognised in the modern literature(50, 97 *a*, 129) as constituting lichen-gonidia are *Trebouxia* (*Cystococcus*) (in Parmeliaceae, Usneaceae, Cladoniaceae), *Chlorella* (recorded in species of *Cladonia*), and *Coccomyxa* (in *Solorina*, *Peltigera*). The record of *Chlorella* requires verification.

Gonidia obtained from the thalli of the same lichen-species growing on diverse substrata also show differences in the colonies formed on nutrient agar, although there is no appreciable diversity observable between the gonidia growing *in situ*. It is of interest that Jaag found that the *Trebouxia*-gonidia of Parmeliaceae isolated in summer show no capacity for further development, while those isolated in spring or winter develop well. In general too growth is better at low than at higher temperatures. Like other Chlorococcales lichen-gonida will grow when supplied with mineral nutriment only in the presence of light, but the growth is poor by comparison to that in media supplied with glucose. In the presence of glucose and peptone they can dispense with photosynthesis and develop normally (4), although organic nitrogen does not appear to be essential for growth (215).

All these facts lend support to the view that the gonidia within the lichen-body lead in part at least a saprophytic existence, being supplied with organic nutriment by the fungus. In any case the work of Chodat and his pupils supports the modern view (cf. (206)) that the alga and fungus associated together in the lichen do not represent a fortuitous assembly, which is readily established by the spores of the lichen being deposited on any growth of *Trebouxia* or other member of Chlorococcales, but that there is an intimate relation between any given lichen-fungus and the appropriate form of the alga with which it consorts. There would appear to be as many types of gonidia as there are species of lichens, but as far as I am aware it has not yet been shown that the alga from a given lichen is able to form a lichen only together with its appropriate fungus and not when spores or hyphae of the fungus from closely allied lichen species are brought together with it. There remains a possibility that the races of *Trebouxia*, for instance, that have been obtained from closely allied lichens, owe their differences to the influence of the fungal partner. In view of the profound physiological changes resulting from the living together of alga and fungus in the lichen, as expressed for instance in the formation of the so-called lichen acids by the latter, this suggestion is perhaps not without force. It is beyond the province of this book to consider further the relation of alga and fungus within the lichen (cf. (129), (206)).

Many of the terrestrial Chlorococcales, in particular, are very commonly found associated with some fungal hyphae without the production of a definite lichen. Acton (1) came to the conclusion that *Botrydina*, commonly found amid mosses, was an example of such a primitive lichen in which a species of *Coccomyxa* was the algal partner. A re-investigation by Jaag (97) has, however, made it probable that the weft of enveloping threads in this case is constituted by the rhizoids of the moss-protonema and that no fungus is present. He believes in a definite partnership between the two organisms (alga and protonema), and this community also includes a species of *Chlamydomonas* which Acton misinterpreted as belonging to the life-cycle of the *Coccomyxa.*

As pointed out above, loss of the green colour is a frequent phenomenon in cultures provided with organic nutriment, and the saprophytic tendency of many Chlorococcales no doubt affords scope for the origin of permanently colourless forms. Such are the *Characium* described by Pascher(157), the genus *Prototheca* (fig. 54 A) of Krüger(115) which appears to be no more than a colourless *Chlorella* ((39) p. 121), and *Hyaloraphidium*(113), a colourless parallel to *Ankistrodesmus*. Hansgirg's *Mycotetraëdron*(84) (fig. 54 B), found on damp walls in a cellar, is possibly a colourless ally of *Tetraëdron*. From a similar habitat Hansgirg(84) has described two other forms (*Myurococcus*, *Myacanthococcus*, fig. 54 C) which probably belong to the Chlorellaceae, although Printz(171) prefers to regard them as colourless Tetrasporineae. It should be emphasised that, as far as our present

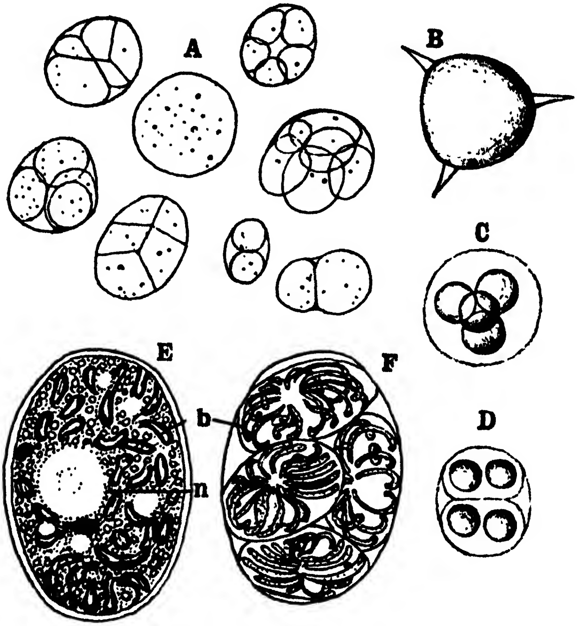

Fig. 54. Colourless members of the Chlorococcales. A, *Prototheca moriformis* Krüg. var. *betulinus*. B, *Mycotetraëdron cellare* Hansg. C, D, *Myacanthococcus cellaris* Hansg. E, F, *Glaucocystis nostochinearum* Itzigs.; E, single cell; F, four-celled colony. *b*, blue-green symbionts; *n*, nucleus. (A after Chodat; E after Geitler; F after Hieronymus; the rest after Hansgirg.)

knowledge goes, all these forms are colourless Algae and that they exhibit no relationship to Fungi except in the absence of pigment.

Of a somewhat different nature is *Glaucocystis* (70). This puzzling alga, long regarded as an anomalous member of the Myxophyceae, appears to be a colourless genus of the Oocystaceae inhabited by symbiotic Blue-green Algae[1] which appear as chromatophores within the cells (cf. *Gloeochaete* among the Tetrasporineae, p. 124). The symbionts appear as a number of curved blue-green bands (fig. 54 F, *b*) grouped in a radiating manner about the conspicuous nucleus, but break up into a number of short rods when the host-cells commence to divide (fig. 54 E, *b*). At present the supposed blue-green symbiont has not been cultivated separately, and it is not impossible that it may have lost the capacity for independent growth. Reproduction of *Glaucocystis* takes place by successive or simultaneous division of the protoplast to form two, four, or eight daughter-cells which acquire membranes of their own and may remain enclosed for a time within the enlarged wall of the parent-cell (fig. 54 F); the latter commonly has polar thickenings at either end. According to Pascher ((156) p. 461) Korschikoff has recorded the formation of swarmers in *Glaucocystis*.[2] Korschikoff (112) has described a similar form, *Glaucosphaera*, with spherical cells enclosed in a wide mucilage-envelope and possessing contractile vacuoles.

A last expression of the saprophytic tendencies of the Chlorococcales is seen in their occurrence as the space-parasites considered on p. 154 and as green cells within the tissues (fig. 55 C, E, F, *a*) of diverse lower animals,[3] a mode of occurrence which is paralleled among Cryptophyceae (p. 658) and Myxophyceae. The occurrence of such green cells has been recorded in most groups of lower animals, perhaps rather more commonly in those inhabiting freshwaters. Thus, they have been found in Infusoria (*Stentor*, *Paramaecium*, *Ophrydium*, etc.), Foraminifera (58), in *Hydra* and other Coelenterata (202), in freshwater sponges and mussels (*Anodonta*, *Unio* (76)), snails, and Turbellarians (74). There is no doubt that in many cases the cells involved are species of *Chlorella* (cf. fig. 55 H, I), often described as *Zoochlorella*. On the other hand various instances are known in which this is not the case. Thus, in *Convoluta roscoffensis* the green cells are due to a *Carteria* (fig. 55 A, B) (101, 102), whilst in other Turbellarians (44) they are constituted by species of *Pleurococcus* (p. 289); the same is true, according to Chodat (51), of the alga in *Ophrydium versatile*. In

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[1] Korschikoff (112) expresses doubts as to the correctness of this interpretation (cf. also (43)). Several cases of the occurrence of symbiotic Blue-green Algae in colourless organisms are, however, now definitely established (156).

[2] It is impossible to consider here the diverse other views that have been held as to the affinities of *Glaucocystis* (see (40), (43), (77)).

[3] See (11), (18), (30), (60). (61), (65), (66), (91), (164–166), (182).

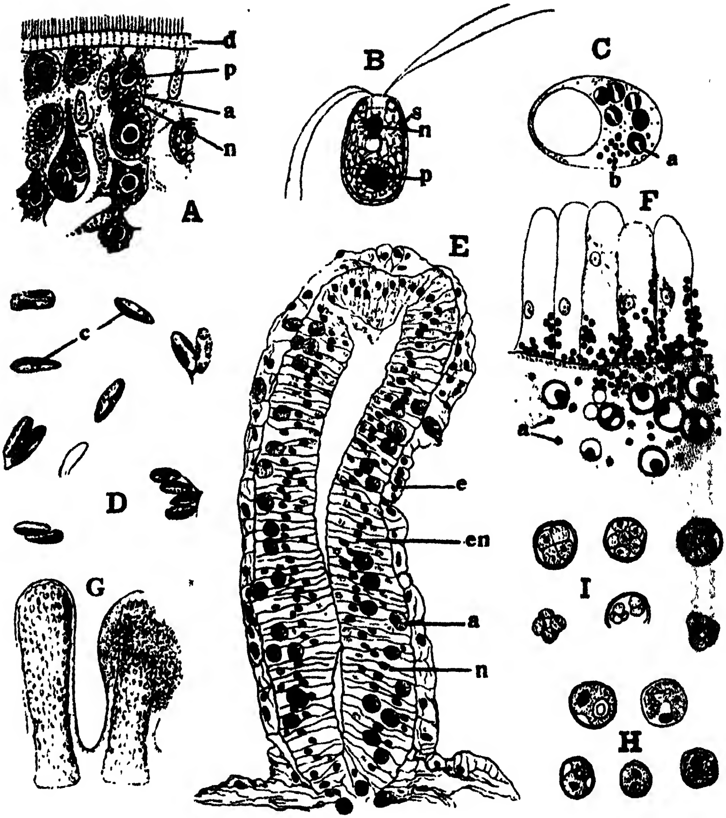

Fig. 55. Green algal symbionts in animals. A, part of a section through the superficial tissues of the marine worm *Convoluta roscoffensis* (after Keeble) showing the position of the green cells (*a*); *d*, the epidermis of the animal. B, Motile cell of *Carteria*, the organism infecting *Convoluta* (after Keeble). C, F, *Zoochlorella* in *Hydra viridis*; C, cell of the endoderm with living (*a*) and disintegrating (*b*) green cells (after Beijerinck); F, section of endoderm (after Hamann), with part of an egg below, into which the green cells (*a*) are spreading. D, *Coccomyxa Ophiurae* Rosenv. and G, two branchial papillae of the Echinoderm *Ophioglypha texturata*, the left hand one normal, the right hand one attacked by the *Coccomyxa* and with the calcareous skeleton partly dissolved (both after Mortensen and Rosenvinge). E, Longitudinal section of the hypostome of the hydroid *Myrionema amboinensis*, with cells of *Chlorella* in the endoderm-cells (*en*) and H, I, *Chlorella* from same; in I in course of reproduction (all three after Svedelius). *c*, chloroplast; *e*, ectoderm; *n*, nucleus; *p*, pyrenoid; *s*, stigma.

diverse Echinoderms species of *Coccomyxa*[1] have been reported as forming the green cells (141, 142). Lauterborn (124) found *Scenedesmus quadricauda* in the freshwater sponge *Carterius stepanowi*, the only case so far known of a colonial form being involved.

Many authorities have affirmed that the *Zoochlorellae* are identical with the common *Chlorella vulgaris*, but even where they closely resemble this alga one will be inclined to suspect different elementary species in the different animal "hosts", just as in the case of lichen-gonidia. So far, however, the culture of the green symbionts outside the animal organism has not been attended with a great measure of success (cf. however (74), (126), (147)). Direct transference from host to host has not been indubitably accomplished. Goetsch and Scheuring (76) state that they were able to infect a *Stentor* with *Chlorella* derived from freshwater mussels, but since they did not work with pure cultures this is open to doubt. Keeble and Gamble (102) report artificial infection of *Convoluta* with the green symbiont. In some cases it has been possible to cause the animals (*Paramaecium*) to adopt the green alga by mixing them with others containing the symbionts or by feeding with *Chlorella* (64, 147, 166, 182), but such experiments have by no means always been attended with success. No doubt diverse Algae are taken up as food, but only the special symbiont can escape digestion and establish itself in the tissues.

As regards the relation between the green cells and their hosts, the presence of the alga seems in the vast majority of cases to be beneficial to the latter. The algal cells, though healthy, rarely contain any accumulation of starch, and it is not improbable that some of the excess carbohydrates are absorbed by the animal. In this connection it is of interest that according to Braarud and Føyn (17) a considerable percentage of the oxidisable organic substance produced in photosynthesis by a marine *Chlamydomonas* diffused into the surrounding culture-solution (cf. also (180)). Moreover, in many cases a certain number of the algal cells within the animal are gradually killed and digested (cf. e.g. (202) p. 45 and fig. 55 C, *b*). The importance of the algal symbiont is illustrated by the fact that Brandt (18) in the case of *Euspongilla* and Pringsheim (165, 166) in the case of *Paramaecium bursaria* showed that these organisms can thrive and multiply in solutions containing no solid food, provided the algal symbiont is present and that the cultures are exposed to light. There is also no doubt that the alga utilises the carbon dioxide produced by the animal, while absorbing further supplies from the water, so that the general effect is to increase the oxygen-content of the medium (211). In the case of *Convoluta* Keeble and Gamble (102) were of the opinion that the green cells, by utilising the products of the animal's nitrogenous metabolism, functioned as an excretory mechanism.

[1] Sokoloff's *Zoocystis* (234) is possibly a *Coccomyxa*.

It does not seem, however, that the relation between alga and animal is normally an obligate one, since in most cases by no means all the animal individuals contain algal cells, and there is no evidence that the colourless forms under normal circumstances thrive less well than those provided with green cells. On the other hand, in the case of freshwater mussels where the algal cells occur only in those parts that are exposed to the light (mantle, gills), Goetsch and Scheuring(76) state that they exert a deleterious influence and they express the opinion that there are probably all stages from a condition of parasitism to one of true symbiosis. A similar case of a *Coccomyxa* causing the death of an Ophiurid has been recorded (141) (cf. fig. 55 G).

There is apparently some diversity in the mode of establishment of the algal partner (29). The gemmulae of the freshwater sponge (*Euspongilla lacustris*), which serve for purposes of propagation, are commonly green ((216) p. 260) and the same is true of the ova (cf. fig. 55 F) and of the buds formed on a *Hydra viridis* (29, 83). Motile stages of Coelenterata appear to be infected before they are liberated (29). In such cases, as in the soredia of lichens, both partners are present from the first, but this is not always so and in many animals the algal cells have to re-establish themselves in every new generation (104). In this connection it is of interest that Wesenberg-Lund (217) reports that in spring the individuals of *Stentor*, in the waters studied, were colourless, whilst in the late autumn they contained numerous *Chlorella*-cells; after the death of the animals abundant *Chlorella* was to be met with in the plankton and these individuals presumably served for a fresh infection in the following season (cf. also (29)). In the case of *Convoluta* the *Carteria*-individuals are attracted chemotactically by the egg-capsules within which they undergo active division.

Symbiosis of a less marked type is reported by Gelei (73), who records the constant presence of *Trochiscia Zachariasii* Lemm. in the mucus enveloping the embryos and larvae of *Rana agilis*. Possibly the frequent occurrence of species of *Characium* on diverse Crustacea and insect-larvae (67, 94) also implies some definite relation between the two organisms. Kammerer (100) describes a similar association between *Oedogonium undulatum* and the larvae of *Aeschna cyanea* and states that he found it difficult to cultivate the former except on an animal substratum, the growth being best on crushed bodies of the larvae. Lipman and Teakle (128) have rendered probable a symbiosis between *Chlorella* and the nitrogen-fixing bacterium *Azotobacter chroococcum*.

THE FAMILY CHLOROSPHAERACEAE

We may follow Printz (171) and Vischer (214 *a*) in including in this family a small number of very imperfectly known Algae which, while otherwise resembling Chlorococcaceae, are distinguished by the occurrence of vegetative division. In *Chlorosphaera* (3, 105, 214 *a*) the thin-walled cells, which possess a typical chlorococcoid structure[1] (fig. 56 E), occur isolated or united to form small groups (fig. 56 F, I) or thread-like expanses (*C. consociata* Klebs, fig. 56 G), which arise as the result of

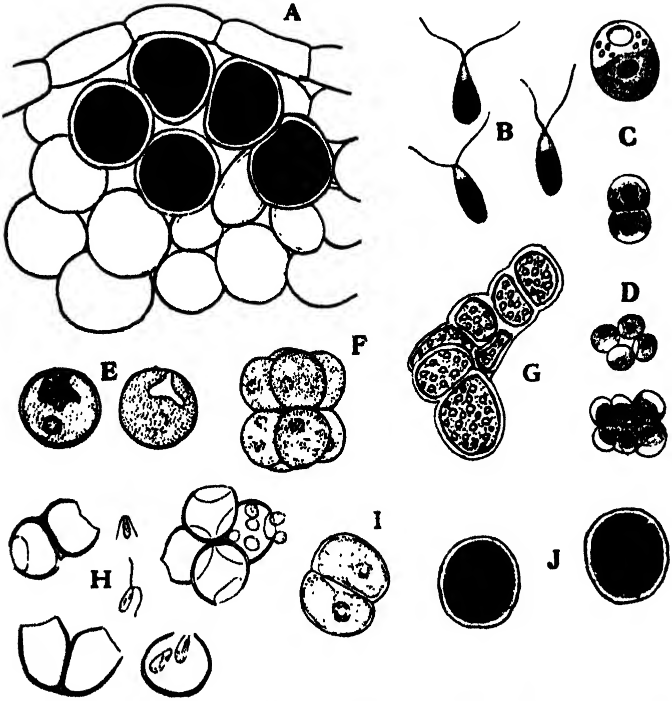

Fig. 56. Chlorosphaeraceae. A, B, J, *Chlorosphaera Alismatis* Klebs; A, cells in the air-spaces of *Alisma Plantago*; B, zoospores; J, divisions leading to formation of same. C, D, *Planophila asymmetrica* (Gern.) Wille. E, F, H, I, *C. Klebsii* Vischer; E, single cells; F, I, packets; H, liberation of zoospores. G, *C. consociata* Klebs. (C, D after Gerneck; E, F, H, I after Vischer; the rest after Artari.)

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[1] In some species the chloroplast may be reticulate, but this hardly appears a sufficient reason for establishing for them a separate genus (*Chlorosphaeropsis*), as Vischer advocates. Gerneck's *Chlorosarcina* (75, 204) cannot be separated from *Chlorosphaera* (cf. (214 *a*) p. 10).

vegetative division in two or three planes. The cells are sometimes endophytic (*C. Alismatis* Klebs, fig. 56 A, in dead leaves of *Alisma Plantago*), but can also occur epiphytically. Reproduction takes place by separation of the individual cells and by means of biflagellate zoospores (fig. 56 B, H); akinetes are also known. Gerneck's *Planophila* (75) (fig. 56 C, D) differs essentially only in the possession of quadriflagellate swarmers. Vischer also inclines to include *Apiococcus* (p. 148) in this family.

The exact position of these forms is at present difficult to establish. *Chlorosphaera* has been regarded by many as possibly being reduced from a filamentous type, mainly because of the tendency to form short threads seen in some species. There is no reason, however, why vegetative division should not have arisen in unicellular forms, and it is not out of the question that the Chlorosphaeraceae may be primitive (cf. (214*a*) p. 93).

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Order III. *ULOTRICHALES*

The faculty of limitless division of a purely vegetative type is the key to the Ulotrichales, as to all other filamentous Algae. There can be no doubt that these originated direct from motile unicells, in the majority of cases at least, the view that assumes a derivation from palmelloid types with a filamentous tendency ((4*a*), (86) p. 372) being altogether unsupported by fact. On the other hand the germination of every zoospore recapitulates the evolution of the filament. In Volvocales and Chlorococcales there is no vegetative division (except perhaps in some Palmellaceae and in the Chlorosphaeraceae, pp. 128, 190), cell-division being always closely linked up with reproduction and involving a rejuvenescence of the protoplast with casting off of the parent-cell membrane at an earlier or later stage. In the filamentous types, on the other hand, a dividing cell is partitioned by a septum which, in many Chlorophyceae, arises as an annular ingrowth from the longitudinal walls and subsequent to nuclear division gradually cuts across the protoplast. The septa may be regarded as affording the necessary mechanical stability for a lengthening cylinder, such as arises from the germinating swarmer (cf. fig. 57 J, K). Should the latter possess the almost spherical chloroplasts that characterise many Volvocales and Chlorococcales, the elongation and septation would give in each cell an annular chloroplast of a hollow cylindrical shape, such as is often realised in *Ulothrix zonata* (fig. 57 A).

The Ulotrichales are characterised by possessing simple unbranched, little differentiated filaments, which in some families give rise to foliaceous expanses. They include a number of separate series which possibly have an independent origin and must be regarded as distinct suborders; these are the Ulotrichineae, the Prasiolineae, and the Sphaeropleineae which are best considered separately.

THE SUBORDER ULOTRICHINEAE

(*a*) The Filamentous Types

The forms included in the family Ulotrichaceae would seem to be the most primitive filamentous types among the Green Algae. The filament is here an unbranched row of cylindrical, uninucleate cells with practically no division of labour, except that the basal cell of the young thread is often developed as an attaching organ (fig. 57 K, *b*) and is then usually deficient in chlorophyll; otherwise all the cells possess the same capacity for growth and formation of reproductive cells. Except in forms inhabiting flowing water, however, the filaments are only found attached in young stages; as they grow longer, they break across at one or more points and thereafter are free-floating. Fragmentation of threads into short lengths, following upon disorganisation of the middle lamella of the septum, remains as a common method of vegetative propagation throughout the period of active growth and attains its height in the terrestrial species of *Hormidium* (fig. 58 H) and *Stichococcus*; in the latter (fig. 59 E, K) there is a great tendency for dissociation of the threads into the individual cells, so that even few-celled filaments are often rare (cf. p. 207).

The species of *Ulothrix* are common in all kinds of freshwaters, *U. zonata* (fig. 57 A, B) being very characteristic of flowing waters, where it forms bright green attached masses, especially in spring and autumn. Several species are marine(53 a, 83, 96), and one of these, *U. flacca* (Dillw.) Thur., is not only often a characteristic form between tide-marks and in the upper part of the littoral zone(22, 96), but also occurs frequently on salt-marshes ((13) p. 356). *U. implexa* is a lithophyte in estuaries ((69 a) p. 55).

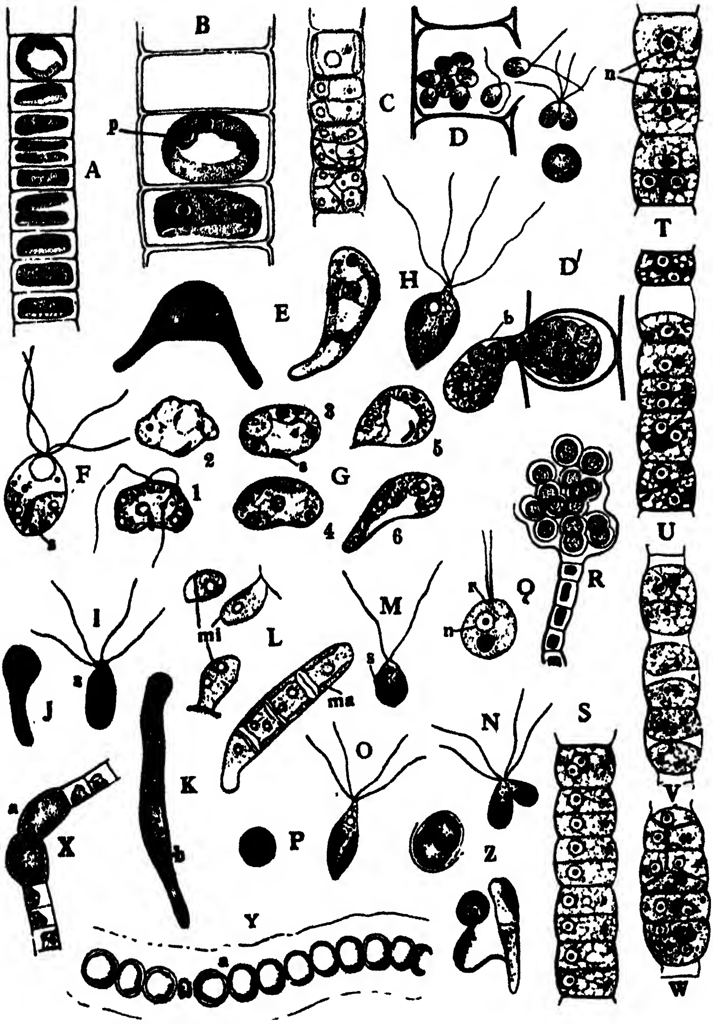

Fig. 57. Structure and reproduction of *Ulothrix*. A, B, D–P, Z, *U. zonata* Kütz.; C, *U. rorida* Kütz.; Q, S–W, *U. variabilis* Kütz.; X, *U. idiospora* West; Y, *U. oscillarina* Kütz. A, B, threads to show form of chloroplast; C, swarmer-formation; D, escape and fusion of gametes; D′, liberation of same; E, germlings of macrozoospores; F, macrozoospore towards end of period of movement; G, *1–6*, successive stages in germination of same (earlier than those in E); H, macrozoospore; I, microzoospore; J, K, germina-

The cells of *Ulothrix*[1] are often shorter than broad or as long as broad (fig. 57 A, B), and, in the wider forms, have thick lamellose walls. The parietal chloroplast, provided with one or several pyrenoids (fig. 57 B), takes the form of a complete girdle in *U. zonata* (at least in the wider threads of this very variable species), whilst in most species of the genus it does not appear to extend round much more than about half the circumference of the cell, although generally occupying the whole length of the latter. In the closely allied genus *Pearsoniella* ((33) p. 314) the annular chloroplasts are in the mature condition produced at their margins into a number of finger-shaped lobes (fig. 58 A).

Lagerheim's *Uronema confervicolum* ((58), (94); cf. also (91 *a*) p. 74) is distinguished from *Ulothrix* by the colourless hemispherical attaching disc secreted by the basal cell (fig. 58 B, *d*), the commonly elongate cells, and the acuminate apex of the terminal cell. Other species that have been described (38, 48) (fig. 58 C) lack one or other of these characteristics, and it remains doubtful whether *Uronema* can really be regarded as an independent genus (7, 35, 48). Some of the other forms certainly seem to link it with *Ulothrix*. The possibility that *Uronema* is a reduced member of Chaetophorales must also be kept in view.

The same uncertainty attaches to the form known as *Schizomeris Leibleinii* Kütz.[2] ((27), (45); cf. also (33) p. 317), which is characterised by the fact that the cells, at first arranged in a single row, undergo division along different planes, so that the threads come to consist of several series of firmly united cells, the whole encased in a firm envelope which appears to correspond to the wall of the original thread (fig. 58 E, F). According to Korschikoff (54) the chloroplast is a coarsely reticulate parietal plate (fig. 58 G). Similar *Schizomeris*-stages are, however, known to occur in species of *Ulothrix* ((19) p. 558) and in *Pearsoniella* (87) and they have also been recorded in *Uronema*-like forms (38). Whatever the validity of *Schizomeris* may be, it is of interest because it shows the tendency to division in more than one plane which is characteristic of the Ulvaceae (cf. p. 212). Korschikoff ((54); cf. also (86) p. 457) would in fact refer it to that family, but this will scarcely meet with general approval.

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[1] See (25), (37), (45).

[2] Watson and Tilden (92) are of the opinion that all the described species belong to *S. Leibleinii*.

tion of same; L, above three germlings from micro- (*mi*) and below a germling from a macrozoospore (*ma*), all of the same age; M, gamete; N, sexual fusion; O, zygote; P, zygospore; Q, gamete; R, palmelloid phase; S–W, stages in formation of swarmers; X, thread with akinetes; Y, the same; Z, germination of zygotes. *a*, akinete; *b*, basal cell; *n*, nucleus; *p*, pyrenoid; *r*, rhizoplast; *s*, stigma. (A, B, original (Miss Rich); C, L after Lind; D, D′, X after West; F, G, after Gross; Q, S–W after Cholnoky; R after Cienkowski; Y after Fritsch; the rest after Klebs.)

The great diversity in type of chloroplast evident in the descriptions of *Ulothrix*, *Pearsoniella*, and *Schizomeris* indicates a need for a careful comparative study of these different forms which may well differ more profoundly in this respect than in the mode of division of the filaments.

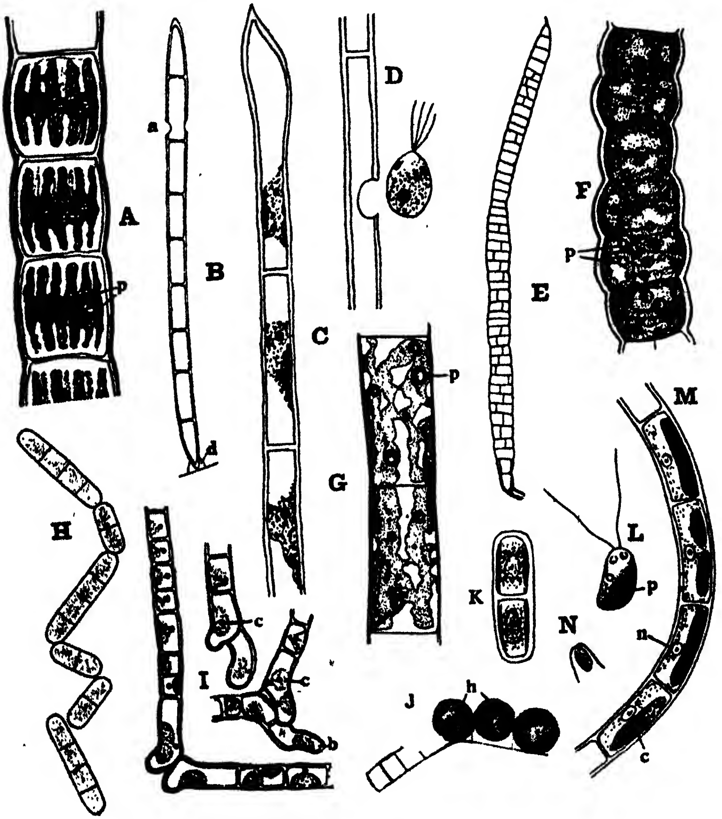

Fig. 58. A, *Pearsoniella variabilis* Fritsch & Rich (after Fritsch & Rich). B, *Uronema confervicolum* Lagerh. (after West). C, D, *U. elongatum* Hodgetts (after Hodgetts); D shows liberation of zoospore. E–G, *Schizomeris Leibleinii* Kütz. (after Korschikoff); E, young thread; F, part of an older one; G, single cells. H, J–N, *Hormidium flaccidum* (Kütz.) Br. (J, N after Wille; the rest after Klebs); H, fragmentation; J, formation of hypnospores (*h*); K, two-celled plant formed from a swarmer; L, zoospore; M, part of a thread; N, gamete. I, *H. rivulare* Kütz., branch-formation and fragmentation (after Hazen). *a*, aperture for escape of swarmer; *b*, branch; *c*, chloroplast; *d*, attaching disc; *n*, nucleus; *p*, pyrenoid.

Apart from the above-mentioned fragmentation, *Ulothrix* reproduces abundantly by means of swarmers whose formation usually commences near the apex and progresses towards the base of the filament.[1] The first indication of swarmer-formation is afforded by the extension of the chloroplast which bends over on to the end walls. This is followed by a slight rounding off of the protoplast which then divides successively (fig. 57 C) into two, four, eight, or more parts. According to Pascher ((71) p. 154) the first division is longitudinal,[2] while according to Gross ((41) p. 223) swarmer-formation is effected by simultaneous division in some species of the genus. The products are liberated through a small aperture formed on one side of the cell (fig. 57 D) into a delicate evanescent mucilage-bladder (fig. 57 D′). In the smaller species it sometimes happens that but a single swarmer is formed from the entire contents of the cell. In *U. variabilis*(17) the cells producing zoospores are described by Cholnoky as being arranged in a linear series, and in all except the last division septa are formed between the products (fig. 57 S–U).

It appears that three types of swarmers may be produced in *Ulothrix zonata*(52, 62, 70), viz. (*a*) quadriflagellate macrozoospores formed in small numbers from the mother-cell, (*b*) quadri- or biflagellate microzoospores, and (*c*) biflagellate gametes, the last two formed in large numbers. The macrozoospores (fig. 57 H) are ovoid in shape, often with a pointed posterior extremity and, according to Klebs, are usually a little flattened; the stigma is anterior and does not project from the surface of the protoplast. The microzoospores (fig. 57 I) are narrowly ovoid, not flattened, and rounded at the posterior end; the stigma lies in the middle of the body and forms a projecting ridge. The gametes (fig. 57 M) are quite similar, though in general smaller and rather more rounded than the microzoospores. According to Klebs ((52) p. 316) and Pascher ((70) p. 26), although the three types of swarmers exhibit transitions in size and in the position of the stigma, the dimensions of each vary about their own mean.

The smaller macrozoospores, however, commonly possess a median stigma, while some of the smaller microzoospores may be biflagellate and others tend to become so by casting off of two of the flagella. Macrozoospores and gametes are the most sharply differentiated types which are scarcely connected by transitions, while the microzoospores stand between and grade over to them in both directions. According to Cholnoky (17) the gametes in *U. variabilis* are formed from potential zoospores which fail to escape and undergo further subdivision to form the sexual swarmers (fig. 57 V, W); he is of the opinion that the gametes of *U. zonata* arise in a like manner.

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[1] See (17), (23), (25), (52), (87*c*), (93) p. 284.

[2] It is, however, noticeable that Klebs ((52) p. 305) figures stages in which only two transversely arranged products are evident (cf. also (41) p. 223).

Macro- and microzoospores are positively phototactic to different light-intensities and can thus be separated ((70) p. 78); moreover, the latter may at low temperatures and in bright illumination exhibit a much longer period of movement (2–6 days) than the former, which usually come to rest within 24 hours and often move for a much shorter period. According to Klebs ((52) p. 319) germination of the microzoospores only takes place at low temperatures (10° C. and below); they develop slowly (cf. fig. 57 L), rounding off on coming to rest, then putting out a rhizoid, and growing into a narrow filament, narrower than that produced from the macrozoospores (fig. 57 J, K). Occasionally the microzoospores develop into resting cells ((70) p. 87). It is noteworthy that Gross (41) was unable to find microzoospores in her material, nor does Cholnoky (17) report them in *U. variabilis*; possibly they are not produced in all habitats. Regel (75) states that in nature they are more particularly formed in the autumn.

The macrozoospores, which no doubt constitute the usual method of asexual propagation, commence to broaden in the last phases of their movement (41) (fig. 57 F), and this continues after a substratum has been reached (fig. 57 G, *1*, *2*), so that the swarmer becomes considerably broader than long. Attachment is effected by the posterior end, and in this connection it is of interest that the stigma shifts to the back end (fig. 57 F) as soon as the broadening of the spore commences. After a membrane has been formed (fig. 57 G, *3*, *4*), the cell grows out laterally at right angles to the original longitudinal axis to form on the one hand the attaching rhizoid (fig. 57 G, *5*, *6*), on the other the ordinary cells of the new filament (fig. 57 E).

The gametes, which are usually liberated in the morning, are isogamous, but fusion normally only takes place between gametes from distinct threads (41),[1] and in many species never occurs when those from a single thread alone are present. The quadriflagellate spindle-shaped zygote (fig. 57 O) soon rounds off to form a spherical thick-walled resting zygospore (fig. 57 P) which according to Dodel (25) may occasionally form a rhizoid-like attaching organ. On germination (25, 50, 52) the contents divide into a number of parts which apparently usually develop as aplanospores (fig. 57 Z); Dodel observed eye-spots and from this concluded a liberation of swarmers, but this has never been confirmed. Gross has shown that reduction occurs at the first division in the zygote, thus confirming the belief that *Ulothrix* is haploid. Parthenogenesis has been induced artificially by Klebs (52), the parthenospores behaving just like the normal zygotes.

During asexual reproduction aplanospores are commonly formed in place of swarmers, and the occasional *Palmella*-stages (fig. 57 R) are obviously but a modification of such aplanospore-formation in which both the parent-membrane and the membranes of the suc-

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[1] According to Lind (62) gametes from adjacent cells fuse in *U. rorida*.

cessive aplanospores become highly mucilaginous. Akinetes are also occasionally produced by thickening, often accompanied by partial gelatinisation, of the walls and accumulation of food-reserves within the cells (fig. 57 X, Y). It is of interest that the same striking diversity of reproductive methods is encountered in *Stigeoclonium*, the central type of the Chaetophoraceae. What is known about the reproduction of *Pearsoniella*(87) and *Uronema* (fig. 58 D) does not indicate any marked difference from *Ulothrix*, while in *Schizomeris* the liberation of swarmers is usually described as taking place from the apex of the filament after breaking down of the cross-walls (cf. however (54)). Sexual reproduction is unknown in these three forms.

The other Ulotrichaceae are even less completely studied. *Hormidium*(7,37,52,72) is often confused with *Ulothrix*, and in the present state of our knowledge the exact limits of the two genera are difficult to define. The extreme forms are, however, readily distinguished. The chloroplast of *Hormidium* is relatively small and in the commonly elongated cells often occupies only about half the length; in shape, moreover, it is typically a circular or elliptical plate (fig. 58 I, M) and thus contrasts markedly with the more rectangular chloroplast of *Ulothrix*. There is a distinct pyrenoid. The colourless cytoplasm at the ends of the cells not uncommonly contains prominent vacuoles enclosing granules of uncertain nature(53).

Reproduction by fragmentation is frequent (fig. 58 H), occurring especially in the terrestrial species, the commonest of which is *H. flaccidum* A. Br.[1] It frequently takes place at points of bending of the threads, so that fragmenting filaments often present a characteristic zigzag appearance. Especially in the aquatic species there is frequent formation of short pseudo-branches (fig. 58 I, *b*), which develop singly or in pairs at points where the threads exhibit knee-shaped bends. In *H. rivulare* Kütz., not uncommon as bright green tufts in flowing water, these branches grow into short rhizoids which are often also found at the ends of the threads. These pseudo-branches are probably merely another expression of the tendency to fragment found in the soil-forms.

Other methods of reproduction are only known in a few species. Characteristic zoospores have been observed in the two above mentioned, as well as in *H. nitens* Menegh.(10, 52), a terrestrial species characterised by the silky glistening strata which are formed by the threads. The zoospores are produced singly from short cells resulting from rapid division, are biflagellate and dorsiventral in structure with a flattened ventral and an arched dorsal surface, against which the chloroplast lies (fig. 58 L). It is, however, not certain that all species of *Hormidium* possess such zoospores.

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[1] Häyrén(44) records this species as abundant on the coastal ice of the Baltic in spring.

Wille (99), in a form of *H. flaccidum*, described aplanospores which either divided to form groups of rounded cells or developed into resting spores with a membrane bearing minute spines (fig. 58 J, *h*). He also recorded ovoid biflagellate gametes (fig. 58 N), otherwise unknown in *Hormidium*. They were formed singly or in twos and were of two slightly different sizes, the larger gametes also developing into short threads directly. Thick-walled resting akinetes have also been observed in some of the species of *Hormidium*.

Other Ulotrichaceae, all possessing a parietal chloroplast, are characterised by an extensive development of mucilage around or between the cells. Thus, in *Geminella*[1] (including *Hormospora* de Brébisson) and *Radiofilum* (80) the threads are provided with a more or less well-marked cylindrical mucilage-sheath which is homogeneous in the former (fig. 59 A, B), but usually exhibits a fibrillar structure at right angles to the longitudinal axis in the latter (fig. 59 J). The mode of origin of this sheath is not clearly established, but it is probably an excretion from the cells. In *Geminella* (fig. 59 A) the cells are generally longer than broad, oblong or ellipsoidal with rounded ends, and are often separated by mucilage; in *G. interrupta* (fig. 59 B) they are commonly placed in pairs which represent the products of a recent division. Most species of *Radiofilum* (fig. 59 G, J) possess cells which are wider than they are long, and the genus is further characterised by the fact that the cell-wall is always composed of two pieces.[2] Not much is known about the reproduction of these two genera, except that vegetative multiplication is the rule; doubtful zoospores are recorded in *Radiofilum* ((80) p. 48).[3]

Binuclearia tatrana Wittr. (81, 82, 101), not uncommon in boggy waters in mountainous districts, is characterised by the marked thickening and prominent transverse stratification of the older septa (fig. 59 H). Cells formed by recent division are thus found in close juxtaposition, while the older ones are more remote. Mature threads often possess a mucilage-envelope. The cells have rounded ends and the usual girdle-shaped chloroplast in which a pyrenoid is not readily distinguishable. Reproduction is usually effected by thick-walled akinetes, which often germinate without separating from one another, their thick ruptured

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[1] Grüss (42) describes a form from the Devonian under the name of *Hormosporites*, which is supposed to be allied to *Geminella*, but the remains figured do not warrant the expression of any definite opinion as to the relationship.

[2] In some respects this genus shows resemblances to the filamentous Desmids (cf. (11)), but the parietal chloroplast speaks against this, as also does the occurrence of zoospores, if their presence be confirmed.

[3] Biflagellate zoospores are also reported in *Gloeotila* ((6) p. 357) which is often included in *Geminella*, whilst other authorities (e.g. (13) p. 165) keep it distinct owing to the absence of pyrenoids and the tendency of the threads to split into short lengths (cf. fig. 59 C, D).

walls forming bands across the threads at intervals (fig. 59 I). Zoospores and aplanospores are also recorded.

The marked tendency to reproduce by fragmentation which is found in many Ulotrichaceae reaches its extreme in *Stichococcus* (7, 16, 37, 40 a), which normally develops only very short few-celled threads in which adjacent cells are usually only in contact along part of their surface. The threads are often found fragmenting into the individual cells

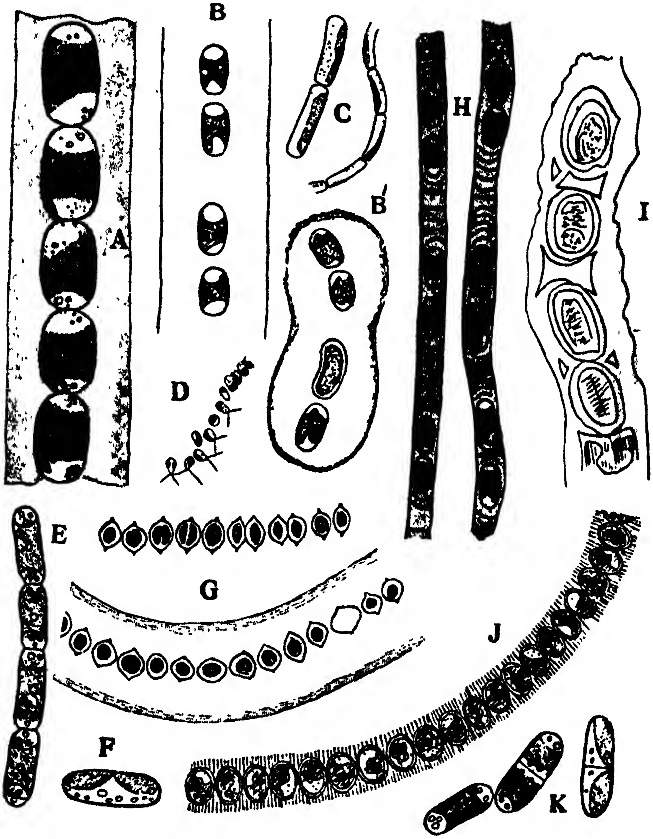

Fig. 59. A, *Geminella mutabilis* (Bréb.) Wille. B, B′, *G. interrupta* Turp.; B, part of a thread; B′, akinetes. C, D, *Gloeotila protogenita* Kütz.; D, swarmers. E, F, K, *Stichococcus bacillaris* Naeg.; E, filament; F, single cell; K, cell-division. G, *Radiofilum apiculatum* West. H, I, *Binuclearia tatrana* Wittr.; I, akinete-formation. J, *Radiofilum flavescens* West. (B after Lagerheim; C after Chodat; D after Borzi; E, F, K after Klercker; G after Bohlin; I after Gutwinski; the rest after West.)

(fig. 59 F, K). The latter are cylindrical with rounded ends, thin walls, and a chloroplast devoid of a pyrenoid[1] (fig. 59 E). Vischer (91) finds that cohesion of the cells depends on the colloidal state (degree of hydration) of the membranes; splitting is favoured by growth in liquid media and by the presence of ions that tend to cause swelling. Nadson (67) has recorded the formation of hypnospores in *S. bacillaris*. According to Chodat (14) this species comprises a large number of elementary species which can be distinguished by their mode of growth in pure cultures. Like many of the Chlorococcales *Stichococcus* thrives best when supplied with carbohydrates in the form of glucose (3, 4, 26, 63, 68).

Microspora

The genus *Microspora* has suffered many vicissitudes. After Lagerheim (57, 59) first clearly distinguished it from *Tribonema*,[2] with which it was long confused, it was regarded as sufficiently distinct from other Green Algae to be placed in an order of its own (Microsporales), whilst in the recent revision of the Chlorophyceae by Printz it is included in the Ulotrichaceae ((73) p. 170), without even being relegated to a distinct tribe. The change of attitude is due to the realisation that its distinctive features do not separate it off as sharply from other Green Algae as was at first thought.

The unbranched threads, found in freshwaters mainly in the colder periods of the year, are composed of cylindrical or slightly barrel-shaped cells with cellulose walls which are sometimes thin, but more usually somewhat thickened and stratified (fig. 60 A). In some (e.g. *M. amoena*), but by no means in all species the walls in the intact threads are clearly composed of two halves (fig. 60 B), which run to a point where the two overlap. According to Neuenstein ((69) p. 42) the halves are held together by a delicate external membrane which is continuous over the thread, while according to Tiffany (90) there is a continuous internal cellulose-layer enveloping the whole protoplast. When such threads disintegrate (or after treatment with 20 per cent. chromic acid), the walls break up into pieces which appear H-shaped in optical section, each such piece consisting of a septum and the halves of the lateral walls of two adjacent cells (fig. 60 D). In the possession of this type of wall-structure *Microspora* resembles *Tribonema*, intermingled with which it often occurs.

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[1] Some species of the genus *Gloeotila* (cf. footnote 3 on p. 206) resemble *Stichococcus* in the absence of a pyrenoid and the occurrence of abundant fragmentation. Here, however, there is also reproduction by zoospores.

[2] Steinecke's contention (87 *b*) of a direct affinity between the two genera cannot be regarded as securely founded. In ordinary habitats, where the two often grow intermingled, they exhibit profound differences.

Printz ((73) p. 159) states that such H-shaped pieces can occasionally also be recognised in the walls of typical Ulotrichaceae (e.g. *Hormidium rivulare*), and Steinecke (87*a*) draws attention to the fact that the edges of the pores, through which the swarmers of an *Ulothrix* escape, are commonly pointed, as if derived from two halves of the wall. It may be doubted, however, whether such features are strictly comparable with the typical bipartite structure of the *Microspora*-wall. In some species (*M. tumidula*) in which this structure is not recognisable in the normal thread, it can be shown to be present by appropriate treatment ((87*b*) p. 220).

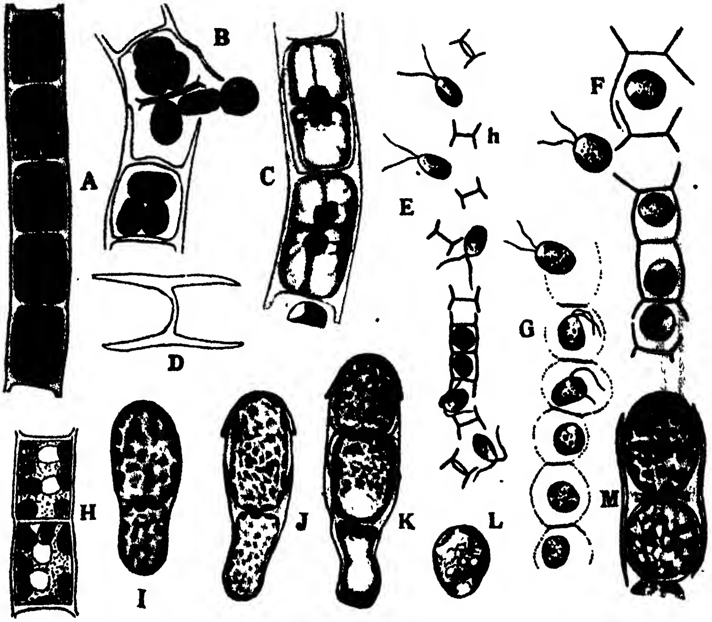

Fig. 60. Structure and reproduction of *Microspora*. A–D, I–M, *M. amoena* (Kütz.) Lagerh.; E, H, *M. tumidula* Hazen; F, *M. floccosa* (Vauch.) Thur.; G, *M. stagnorum* (Kütz.) Lagerh. A, thread; B, formation and liberation of zoospores; C, early cleavage in swarmer-formation; D, H-piece; E, liberation of swarmers, H-pieces (*h*); F, the same; G, the same, gelatinisation of walls; H, chloroplast-structure; I–K, stages in germination of aplanospores; L, aplanospore; M, formation of the latter. (A, E–H after West, the rest after Meyer.)

The chloroplast of *Microspora* ((93) p. 289, (64)) is parietal and appears normally to occupy the whole peripheral cytoplasm, even extending over the end-walls of the cells. It is usually of uneven thickness, being thickened at certain points to form cushions (fig. 60 H), and is often more or less reticulate in character (fig. 60 A); in some species (e.g. *M. Willeana*) it appears to consist of a number of loosely connected bands which are often moniliform in nature. There are never any pyrenoids, but small starch-grains are often present. There is a single central nucleus, which is often large and distinct; its structure and division have been studied by Neuenstein and Cholnoky(18, 69) (cf. fig. 10 L–P).

As in *Ulothrix*, diverse kinds of swarmers are known. The usual type is ovate and biflagellate (fig. 60 E–G). These swarmers are produced generally to the number of one or two[1] per cell, being set free by disintegration of the walls into their H-shaped components (fig. 60 E, F) or by gelatinisation (fig. 60 G) of the cell-membranes ((93) p. 290). In addition quadriflagellate zoospores are recorded in *M. Willeana* (64). These two kinds of swarmers appear to be definitely asexual. Apart from these, pear-shaped or elongate biflagellate swarmers, from 2 to 16 of which are formed in each cell, have been observed in some species and these are possibly gametes (88, 93). Fusion has been recorded by Steinecke(87 *b*) in *M. tumidula* where the gametes are stated to have unequal flagella. All three types of swarmers can develop as aplanospores (fig. 60 M) and, when formed singly, such structures often develop into hypnospores(95). Thick-walled akinetes, square or rectangular in optical section, generally arranged in long chains, are not uncommonly produced.

In the germination of the zoospores or aplanospores(64, 93) the first division is by a normal septum, the smaller of the two resulting cells playing no further part in the development of the thread and probably corresponding to an attaching cell, even when not functional (fig. 60 I). In those species which possess the H-structure, this is developed at the second division by transverse rupture of the wall subsequent to the apposition of an internal cylindrical strip of membrane; from the middle of the latter a septum gradually grows across the cell-cavity (fig. 60 J, K). In other cases normal transverse division appears to continue throughout the life of the filament ((93) fig. 185 H–J).

Microspora shows sufficient peculiarities (chloroplast, wall-structure, absence of pyrenoids) to warrant keeping it for the present in a distinct family, Microsporaceae.

Cylindrocapsa

In the few forms so far considered in which sexual reproduction has been observed, this is essentially isogamous, and in this respect there is correspondence with the simple vegetative status (simple chloroplasts, lack of division of labour between the cells, the unbranched

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[1] Sometimes, however, in larger numbers (cf. fig. 60 C).

habit). In the rare *Cylindrocapsa* ((19), (86) p. 388, (93) p. 291), however, we have well-marked oogamy, despite the fact that the vegetative structure is so little different from that of the Ulotrichaceae that it is often included in this family. The threads of *C. involuta* Reinsch (fig. 61 A) consist, when young, of a row of elliptical cells with thick stratified walls and a parietal, massive, often ill-defined chloroplast containing a single pyrenoid, the whole enclosed in a close-fitting sheath. In the older threads longitudinal and oblique division-walls arise in the cells, so that the latter exhibit an irregular arrangement (fig. 61 B). Spherical or ovoid biflagellate zoospores are formed singly or to the number of 2–4 in the cells or their place may be taken in the usual way by aplanospores. Detachment of single cells or groups of cells which grow out to form new threads has also been observed.

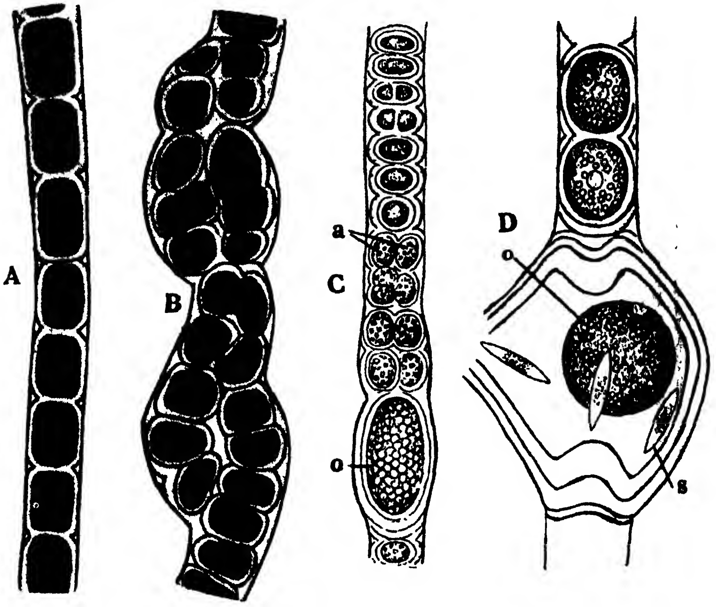

Fig. 61. Structure and reproduction of *Cylindrocapsa involuta* Reinsch (after Cienkowski). A, normal thread; B, older stage of same; C, thread with antheridia (*a*) and a young oogonium (*o*); D, mature oogonium with ovum (*o*) and spermatozoids (*s*).

The antheridia (fig. 61 C, *a*) are produced by active division of certain cells and are arranged in one, two, or four longitudinal series within the sheath. Each gives rise to two elongate biflagellate spermatozoids (cf. fig. 61 D, *s*) of a brownish red colour, which are liberated by rupture or gelatinisation of one side of the membrane. The oogonia (fig. 61 D) are represented by much enlarged spherical or ovoid structures with a thick stratified wall which opens by a rather wide lateral pore. The single ovum (*o*) is formed by contraction of the protoplast and, after fertilisation, acquires a thick wall and brick-red contents. Germination of the oospore has not been observed, but parthenogenesis, in which the green ova divide into 2–4 cells which grow into new threads, has been recorded(19).

In its sexual reproduction *Cylindrocapsa* shows considerable resemblances to *Oedogonium*, but it may be doubted whether this implies any actual affinity.

(*b*) THE THALLOID TYPES (ULVACEAE)

An advance in vegetative construction on the forms hitherto discussed is seen in the Ulvaceae which are distinguished by the production of a parenchymatous thallus as a result of the division of the cells in more than one plane. Unlike the other Ulotrichineae they are essentially marine, occurring mainly in the littoral zone or near low-tide level. Species of *Enteromorpha* and *Monostroma* are, however, found in freshwaters, and several of the marine *Enteromorphas* (e.g. *E. compressa* Grev.) and *Ulvas* are capable of existing in a rather wide range of salinities, often ascending some distance into estuaries, especially when there is some pollution. Cotton (21) has shown that *Ulva Lactuca* var. *latissima* thrives in sewage-polluted waters and under these conditions contains an increased amount of nitrogen. Species of *Enteromorpha* (e.g. *E. compressa*) and *Ulva* commonly occur in the upper part of the littoral zone on rocky shores and are often found where supplies of fresh water escape from the cliffs ((22) p. 22, (40), (53 *a*)).

Except in *Monostroma* the young plants consist of a basally attached filament (figs. 62 A, 64 L–N) which is often very much like that of a species of *Ulothrix* (78, 89). Longitudinal division sets in at an earlier or later stage (fig. 62 C) and leads to the formation of a two-layered expanse which becomes broad and flat with the two layers in close contact in the cosmopolitan genus *Ulva* (sea lettuce, fig. 62 E) and the extra-European *Letterstedtia* (fig. 63 A). In *Enteromorpha*, on the other hand (fig. 63 B), the two layers separate at an early stage and subsequently divide only by walls at right angles to the surface, forming long intestiniform tubes with a one-layered wall. Growth in *Enteromorpha* is partly effected by an apical cell which divides by transverse and longitudinal walls into segments which increase the length of the thallus ((73) p. 173). The latter, however, also enlarges by intercalary division. The branches, common in various species of *Enteromorpha*, likewise grow partly with the aid of an apical cell which arises promiscuously from any cell of the main axis. In *Letterstedtia*(1) the thallus is not as broad as in *Ulva* and is usually extensively branched, the various branches bearing many small serrations which arise as outgrowths or as a result of tearing of the margin (fig. 63 A).

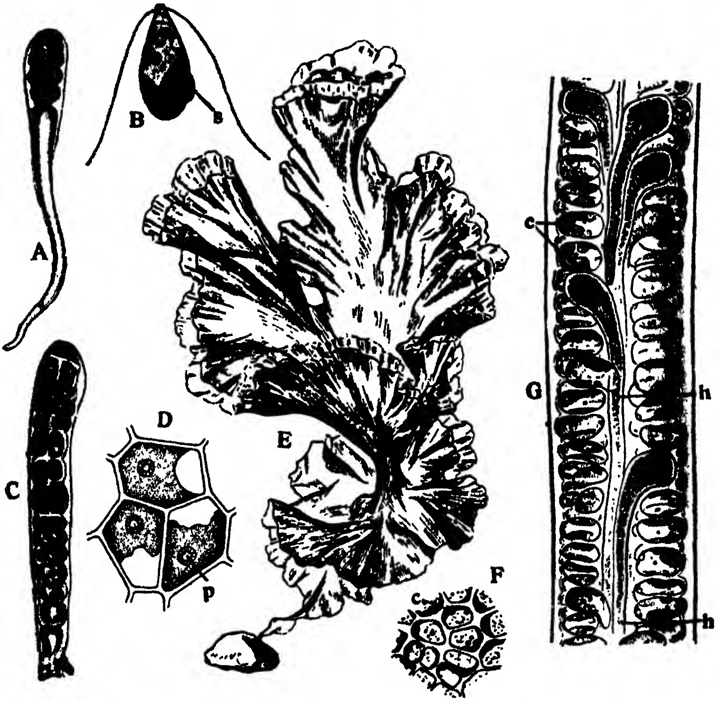

Fig. 62. Structure and reproduction of *Ulva Lactuca* L. A, C, young plants; B, parthenospore; D, cell-structure; E, habit; F, small part of thallus; G, longitudinal section of mature thallus. *c*, chloroplast; *h*, rhizoids; *p*, pyrenoid; *s*, stigma. (A–C after Schiller; D after Schimper; E, G after Thuret; F after Fritsch & Salisbury.)

In the case of *Monostroma*(12,76,77,100) the zygotes divide into eight peripherally arranged cells enclosing a central cavity (fig. 63 G, H); by gradual enlargement a vesicular thallus is produced, which at an earlier or later stage opens out to form a one-layered expanse, whose origin from a vesicle can often still be detected in the basal region.[1]

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[1] Chodat(15) gives a rather different account, which has not been confirmed (cf. fig. 63 E, F).

All Ulvaceae are primarily attached to a substratum, *Ulva* and *Enteromorpha* often throughout life. The basal part of an *Ulva* is narrowed into a short stalk, dilating into a more or less marked attaching disc (fig. 62 E). The latter is formed from the primary attaching cell (fig. 62 A) strengthened by numerous multinucleate rhizoids that grow out from the lower cells of the thallus and broaden out at their tips adjacent to the substratum(24, 89). These rhizoids in part push their way between the two layers of the thallus (fig. 62 G, *h*), in part penetrate to the exterior and appear as interwoven strands apposed to the stalk. According to Schiller(78) some of these rhizoids may develop into green filaments producing secondary thalli, hence the frequent tufted growth. Both in *Enteromorpha*(4 *b*) and *Ulva* new thalli may also arise from the mature attaching discs, which appear to be perennial in the case of some species of *Ulva*, while the laminae become disorganised at the end of each season. When *Ulva* grows attached to other seaweeds, some of the rhizoids may penetrate between the cells of the substratum. Similar rhizoids are also known in *Enteromorpha* and *Monostroma*(100).

The cells are usually placed with their long axes at right angles to the surface of the thallus (fig. 62 G). They contain a single parietal chloroplast, often with deeply incised or lobed margins and including a single pyrenoid (fig. 62 D, F). The chloroplast is mostly located on the outer side of the cell, while the nucleus lies adjacent to the inner wall; darkening of *Ulva Lactuca* leads to a shifting of the chloroplast to the side-walls(84). According to Henckel the chloroplast in *Enteromorpha intestinalis* always lies against the lower side of the cell(47). The cell-walls are generally distinctly stratified.

Vegetative reproduction may be effected by detached fragments of the thalli. This occurs commonly in *Ulva* and may lead to the formation of loose-lying communities(79), while Carter ((13) p. 347, (13 *a*)) records unattached forms of *Enteromorpha* on salt marshes. In *Monostroma bullosum* detachment of marginal groups of cells or of specially differentiated akinetes has been observed. Zoospores, which are as a rule quadriflagellate (fig. 64 I) and are formed by successive division of the contents of any of the ordinary cells into 4–8 parts, are known in all genera; they are liberated through a hole formed in the wall.

Sexual reproduction is known in *Monostroma*(12, 15, 66), *Ulva*(5, 28, 78), and *Enteromorpha*(2, 4 *b*, 43, 55), all of which appear normally to be dioecious, only gametes from distinct plants conjugating with one another.[1] In the case of the two last-named genera it has, moreover,

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[1] Schiller ((78) p. 1702), however, records copulation between the gametes while still within the parent-cell, although he was unable to follow up the further development of such zygotes. According to Bliding(4 *b*) *Enteromorpha Linza* and *E. procera* possess only asexual swarmers.

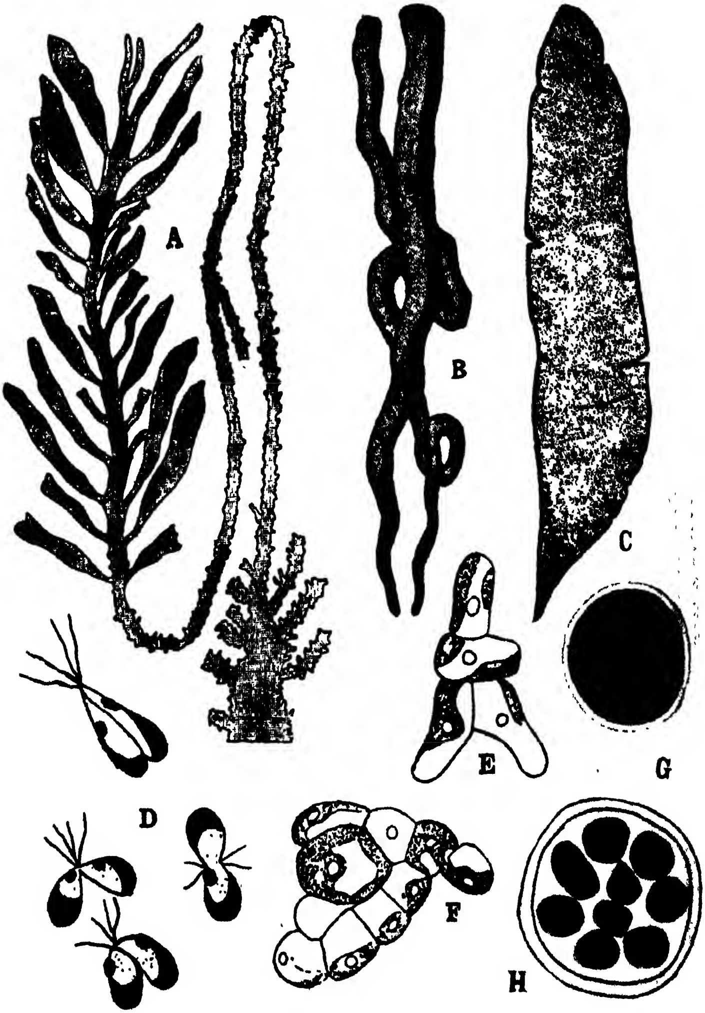

Fig. 63. A, *Letterstedtia insignis* Aresch. B, *Enteromorpha intestinalis* (L.) Link. C–H, *Monostroma*; C, *M. membranaceum* West; D–H, *M. bullosum* (Roth) Wittr.; C, habit; D, fusion of gametes; E–H, development of zygote. (A after Areschoug; B, C after West; D, G, H after Reinke; E, F after Chodat.)

been shown(4 b, 28, 43) that there is a regular alternation between a diploid asexual and a haploid sexual generation, the two resembling one another in all outward respects. Reduction, although not yet fully established on a cytological basis, no doubt occurs at the first division in the formation of the zoospores. The gametes are biflagellate (figs. 63 D, 64 A, B) and are formed in any cell in the same way as the zoospores, usually to the number of eight; they are smaller than the zoospores. Those of *Ulva* have a prominently projecting posterior stigma (fig. 62 B). Swarmer-formation usually takes place over extensive areas of the thallus, commonly proceeding inwards from the margin, the portions that have already discharged their contents appearing white.

When gametes of different strains are brought together dense aggregates are formed, as in other isogamous Algae. The gametes usually show pronounced positive phototaxis, but immediately after fusion the reaction changes to a negative one(12, 28, 55, 66). In most cases there are appreciable variations in size among the gametes, but except in *Enteromorpha* (especially *E. intestinalis*) there appear to be no constant differences between the two sexes. Carter(12), however, states that the female gametes of *Monostroma* are on the whole slightly larger than the male (cf. also (103) p. 109). In *Enteromorpha intestinalis*, male plants are according to Kylin(55) readily distinguished with the naked eye by the orange-yellow colour of the fertile portions, while in the female plants these are yellowish green and not so distinctive. Both kinds of gametes are pear-shaped (fig. 64 A, B), but the male are smaller and narrower; they possess a pale yellowish green chloroplast with a rudimentary pyrenoid, while in the female gametes the chloroplast is green and has a distinct pyrenoid. The zygote (fig. 64 F) at first contains two chloroplasts, but that of the male soon disorganises. The gametes of Ulvaceae apparently readily give rise to parthenospores which behave like the sexually produced zygotes (cf. (12), (78)); according to Schiller those of *Ulva* arise from gametes larger than the normal ones. In the case of *Enteromorpha clathrata* Bliding(4 b) found that such parthenogenetic gametes gave rise only to plants of their respective sex. There would seem to be some variability with respect to the behaviour of the spores, since some observers record immediate germination, whilst others speak of a resting period.

The fact that the Ulvaceae exhibit isomorphic (homologous) alternation, whereas in *Ulothrix* the diploid generation is represented only by the zygote, is quite in conformity with the higher vegetative differentiation of the former. The Ulvaceae are clearly an advance on the Ulotrichaceae, the direction of which is indicated by the *Schizomeris*-stages of *Ulothrix* (p. 201). It is of very considerable interest that the point of the reduction division has been shifted in correspondence with this vegetative advance. There can be little doubt that the Ulvaceae have originated from filamentous types, in view of the fact that the majority start life as a simple filament. Young stages of *Enteromorpha* are scarcely to be distinguished from *Ulothrix*. Even in *Monostroma* it would seem that the early stages are sometimes filamentous (15). The placing of the Ulvaceae in a separate order (86, 93) is therefore scarcely warranted. The view that relates Ulvaceae and Tetrasporaceae has no basis in fact. It is of interest that parallel types occur both in Brown and Red Algae, and these too are referable to a filamentous ancestry.

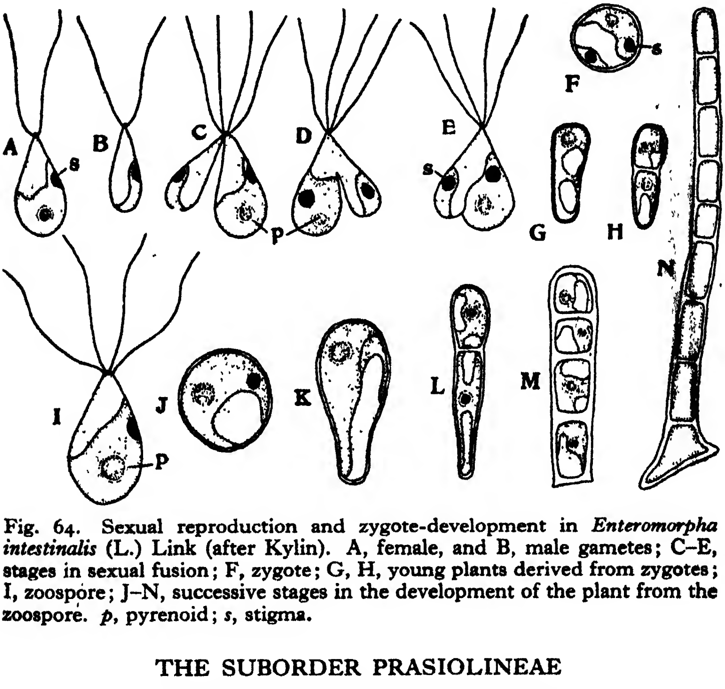

Fig. 64. Sexual reproduction and zygote-development in *Enteromorpha intestinalis* (L.) Link (after Kylin). A, female, and B, male gametes; C–E, stages in sexual fusion; F, zygote; G, H, young plants derived from zygotes; I, zoospore; J–N, successive stages in the development of the plant from the zoospore. *p*, pyrenoid; *s*, stigma.

THE SUBORDER PRASIOLINEAE

By contrast to the parietal chloroplast which characterises all the preceding forms, the genus *Prasiola*[1] has an axile stellate chloroplast with a large central pyrenoid in each cell (fig. 65 D); there is a single nucleus. Species of the genus occur both subaerially, as well as in fresh and salt water.

The early stages commonly consist of a simple unbranched filament with flat cylindrical cells (36) and relatively thick longitudinal walls (the *Hormidium*-stage, fig. 65 B, C (lower part), E), and this may

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[1] See (8), (37), (49), (60), (96–98).

remain the condition throughout life. Usually, however, longitudinal divisions set in sooner or later and lead to the formation of two or four longitudinal rows of cells (*Schizogonium*-stage, fig. 65 C) or of a more or less expanded and often irregular foliaceous thallus, mostly consisting of a single layer of cells (fig. 65 A, B). In these expanded thalli the cells are small, quadrate or polygonal in outline, and generally elongated at right angles to the surface; they are commonly very regularly arranged in groups of four, larger or smaller aggregates of which are separated by thicker walls in a characteristic manner. Short rhizoids may grow out from the cells of the lower, often stalk-like portions of these thalli; these rhizoids may be cut off by a wall from the parent-cell and may grow out into short multicellular threads Similar rhizoids are sometimes produced by the marginal cells of the leafy expanses.

Reproduction takes place in the filamentous stage by fragmentation, usually brought about by the dying of isolated cells which appear at first as deep green biconcave structures with homogeneous contents. In the leafy thalli budding often occurs from the margins, leading to the detachment of single cells, short threads, or small expanses. Large, round thick-walled akinetes (fig. 65 E) are also formed which can grow directly into new plants or on germination give rise to a number of aplanospores (fig. 65 F, G) from which the new plants are produced (98). There is no certain evidence of the occurrence of swarmers. Yabe (102) has recently described a sexual reproductive process in *P. japonica*, the biflagellate gametes being of two sizes and formed by division of the cell-contents along three planes. No evidence is produced, however, that the swarmers shown in the figures are actually liberated from the *Prasiola*-cells, nor do the former show the structural features typical of the genus. For the present, therefore, the occurrence of such reproduction, whilst not necessarily improbable, must await more definite substantiation.

The common terrestrial species, *Prasiola crispa*, which occurs also in the spray zone on rocky shores, exhibits a very varied differentiation in different habitats. Under certain conditions (e.g. under the shade of trees) the filamentous stage may persist indefinitely. At other times the cells may undergo radial and tangential longitudinal division (cf. (73) p. 181) (fig. 65 H, I), a form which has been described under the name of *Gayella polyrhiza* and is regarded by many as belonging to a distinct genus ((77) p. 936, (85) p. 279). The leafy expanses are commonly met with under walls and forming a green carpet between the paving stones of quiet streets. *P. fluviatilis* is met with in cold streams, while *P. stipitata* and *P. furfuracea* are examples of commoner marine forms, the former being often distinctive of the upper part of the littoral zone ((69a) p. 79).

The terrestrial species favour habitats in which there is a con-

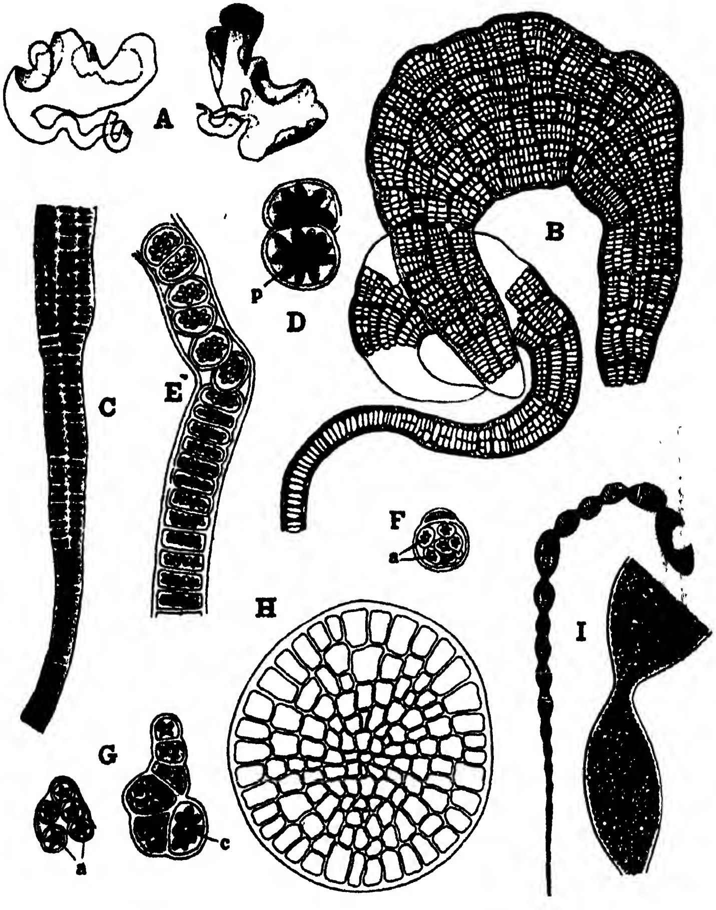

Fig. 65. The genus *Prasiola*. A–C, E, F, *P. crispa* (Lightf.) Menegh.; D, G, *P. furfuracea* (Mert.) Menegh. A, habit; B, the same, two plants enlarged; C, *Schizogonium*-stage of forma *muralis*; D, cell-structure; E, "*Hormidium*"-stage with akinetes; F, germinating akinete with aplanospores (*a*); G, on the left germinating akinete with aplanospores (*a*), on the right young plant with aplanospores. H, I, The form known as *Gayella polyrhiza* Rosenv.; H, section of an old thallus; I, habit. *c*, chloroplast; *p*, pyrenoid. (A, B after Imhäuser; C–E after Gay; F, G after Wille; H, I after Setchell & Gardner.)

siderable accumulation of nitrogenous organic matter[1] and occur, for example, in prodigious quantities in the neighbourhood of the penguin rookeries in the Antarctic. The subaerial forms are capable of withstanding very considerable desiccation in the ordinary vegetative condition, a faculty which appears to be related to the absence of conspicuous vacuoles in the cells and a high degree of viscosity of the protoplasm(30, 32).

In spite of the superficial similarity to Ulvaceae, there is little probability of any direct relationship in view of the contrasting cell-structure. Forms with axile and more or less stellate chloroplasts are known both in Volvocales and Chlorococcales, and it is possible that they belong to a distinct, little developed series of which *Prasiola* represents the filamentous and thalloid differentiation. The relation between *Prasiola* and some of the *Trebouxia*-like forms met with on terrestrial substrata in nature has still to be established; it is not impossible that certain of the latter represent unicellular stages in the life-cycles of species of the former genus (cf. (9)). There is much superficial resemblance between *Prasiola* and the Bangiaceae among the Rhodophyceae, especially the species of *Porphyra*. The record of Lagerheim (60) of the formation of "tetraspores" by vertical and horizontal division of enlarged rounded cells in *Prasiola mexicana* J. Ag., an observation that awaits confirmation, has led to a common belief in the existence of a relationship between the two sets of forms. There can be no doubt, however, that the resemblances are solely due to parallel development, since the pigments in the chromatophores and the assimilatory products are quite different in the two groups (56).

THE SUBORDER SPHAEROPLEINEAE

To this suborder belongs the solitary genus *Sphaeroplea*,[2] the species of which are widely distributed over the surface of the earth, though mostly of rather localised occurrence. The most usual habitat appears to be periodically inundated ground, and the period of vegetative activity would often appear to be rather short.

Sphaeroplea occurs in the form of long unbranched filaments which are free-floating from the first. The threads consist of a number of often greatly elongated coenocytes (fig. 66 A, B), a feature which is responsible for the usual reference of the genus to the Siphonales. Each coenocyte normally contains a number (from one or two up to 70 in extreme cases) of annular parietal chloroplasts in the shape of narrow bands with smooth or more or less denticulate margins and with a limited number of pyrenoids arranged in a single series (fig.

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[1] Letts (61) has shown that specimens of *Prasiola* growing on contact-beds may contain as much as 8·94 per cent. of nitrogen in the dried material.

[2] See (20), (29) p. 524, (31), (34) p. 36, (39), (46), (65), (74).

66 A). Each such chloroplast occupies the periphery of a concave disc of cytoplasm which extends transversely across the coenocyte; these discs divide up the central cavity into a succession of large vacuoles (104) alternating with the chloroplasts. The successive green rings are usually quite distinct from one another, although reticulation

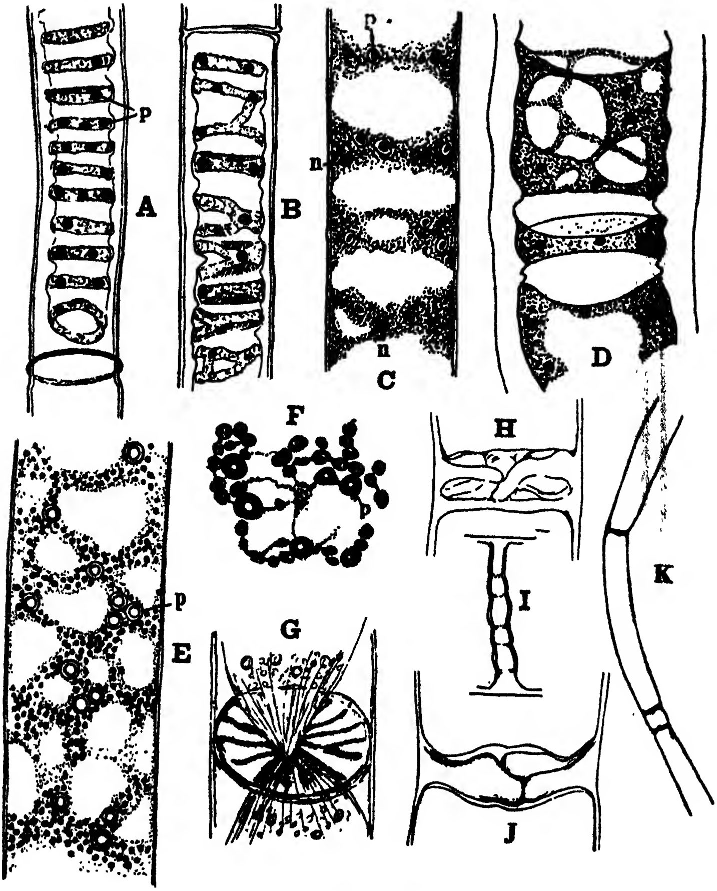

Fig. 66. Vegetative structure of *Sphaeroplea* (C after West, the remainder after Fritsch). A–C, *S. annulina* (Roth) Ag.; E, G–K, *S. africana* Fritsch; D, F, *S. africana* var. *crassa*. A–C, E, structure of coenocytes; D, reticulation of annular chloroplast; F, part of mature chlorophyll-apparatus of var. *crassa*; G–J, septa, in G in surface-view; K, part of thread with a very short segment. *n*, nucleus; *p*, pyrenoid.

of individual chloroplasts, especially during division, is not uncommon (fig. 66 D). In certain very wide forms (e.g. *S. africana* var. *crassa*) the entire chlorophyll-apparatus of the coenocyte comes to be of the nature of a diffuse network in which large numbers of pyrenoids are irregularly scattered (fig. 66 F). That this is a derivative condition from that normally found in the narrower species is shown by the fact that young threads in all cases possess separate annular chloroplasts[1] and that these may persist locally in parts of occasional coenocytes. In the wide forms with a reticulate chloroplast, fragmentation of the latter is a frequent phenomenon. Such reticulation and fragmentation appear invariably to occur in coenocytes which are preparing to produce ova (cf. below and fig. 67 D).

In the forms with annular chloroplasts the nuclei are practically confined to the cytoplasmic discs, lying internal to the chloroplasts; they are few in number in each disc, often only two, sometimes only one. On the other hand in the coenocytes with reticulate chloroplasts the nuclei are quite irregularly scattered.

The septa are often peculiar and complex. In the narrower forms the normal septa would seem to be homogeneous ingrowths (fig. 66 A) from the longitudinal walls, but in *S. africana* they are composed of a series of radial processes (fig. 66 G). The latter, moreover, commonly fail to meet at the centre, so that the cytoplasm extends continuously from one coenocyte to another through the central aperture (fig. 66 G). Such septa would appear also to occur occasionally in most of the other species and, where these develop thick septa, thickening is often due to the production of irregular processes on either side of the original septum (fig. 66 H, J). It would rather seem as though normal septation is disappearing altogether in *Sphaeroplea* and being replaced by groups of radial strands, somewhat comparable to the strengthening strands of a *Caulerpa* (p. 382) and perhaps fulfilling a purely mechanical function.

Apart from fragmentation, only sexual reproduction is known in *Sphaeroplea*, but this is very prolific. The vegetative segments constitute oogonia and antheridia without any change of form, in which respect *Sphaeroplea* is unlike any other oogamous green alga and stands on no higher level of differentiation than the majority of isogamous types. The threads are either monoecious or dioecious and the sexual organs are developed singly or in short series. In the oogonia(20, 51) the annular arrangement of the green pigment gives place to a reticulate arrangement and the entire protoplasm of the segment becomes gradually cleft (fig. 67 C) into numerous spherical ova, provided with a colourless receptive spot, deep green contents and a number of pyrenoids (fig. 67 E). There is no nuclear division

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[1] According to unpublished observations of Miss Talbot.

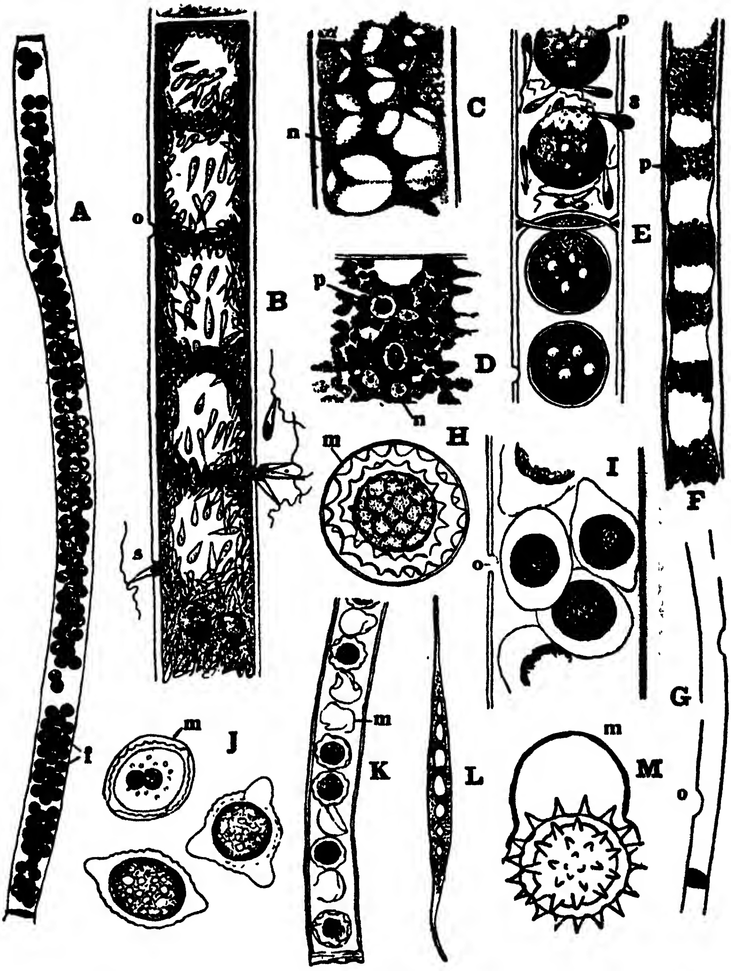

Fig. 67. Sexual reproduction of *Sphaeroplea*. A, I, J, *S. africana* Fritsch; B–E, H, *S. annulina* (Roth) Ag.; F, G, M, *S. tenuis* Fritsch; K, *S. Wilmani* Fritsch & Rich. A, a large oogonium; B, formation and liberation of spermatozoids; C, segmentation in the oogonium; D, part of a green band (probably early reproductive stage); E, above, ova at time of fertilisation; below, two zygotes; F, vegetative segment; G, the same with pores; H, mature oospore before escape from primary membrane; I, young zygotes in oogonium; J, mature oospores; K, part of oogonium, shedding of primary membrane of zygote; L, germling from a zoospore; M, probable zygote escaping from primary membrane. *f*, ovum; *m*, primary membrane of zygote; *n*, nucleus; *o*, aperture of oogonium or antheridium; *p*, pyrenoid; *s*, spermatozoid. (B–E after Klebahn; H, K after Fritsch & Rich; L after Cohn; the rest after Fritsch.)

during the formation of the ova and the latter are normally uninucleate. Occasionally a small part of the protoplasm is not utilised in the formation of the ova and remains behind as a shrunken mass. The numerous ova are arranged in a single series (fig. 67 E) or more commonly in several longitudinal rows (fig. 67 A).

In the developing antheridium the annular arrangement of the contents remains recognisable until a late stage (fig. 67 B). Abundant nuclear division occurs, the pyrenoids gradually become indistinct and finally disappear, while the chloroplasts become cleft into numerous minute parts and assume a reddish yellow colour (fig. 67 B). The mature spermatozoids are uninucleate, of a narrow elongate form, and possess two apical flagella and a small yellowish plastid.

The spermatozoids are liberated through a number of small round or somewhat irregular holes (*o*), which form in the longitudinal walls of the antheridia (fig. 67 B), and similar apertures arise in the oogonial walls to allow of the entry of the spermatozoids in fertilisation (fig. 67 E, I, *o*). In all cases the fertilised ovum becomes enveloped by a close-fitting, smooth and thin, hyaline membrane, within which the two permanent membranes are gradually laid down (fig. 67 H, J, *m*). When these are formed, the primary membrane is shed, and in ripe oogonia such empty membranes are to be found in large numbers lying alongside of the mature oospores (fig. 67 K, *m*). The latter are either spherical (fig. 67 H, K) or provided with a number of conspicuous wing-like ridges (fig. 67 J) and the outer membrane is ornamented in diverse ways; the contents are coloured brick-red. The mature oospore is uninucleate (39).

The germination of the oospores has only been observed in *S. annulina* (46, 65). As a general rule the contents divide to form four biflagellate pear-shaped swarmers, although smaller numbers are sometimes found. They commonly retain part of the red pigment of the oospore and are stated to develop a membrane during movement. Ultimately they come to rest without reaching a substratum. The body of the swarmer then lengthens to form a spindle-shaped filament which may reach a considerable length before the first septum is formed (fig. 67 L). It can hardly be doubted that reduction occurs at the first division in the oospore. *Sphaeroplea* is unique among the Green Algae in the formation of swarmers from the germinating zygotes, although they are not known to be produced by the ordinary vegetative threads.

Sphaeroplea occupies a primitive position among the oogamous Green Algae in the fact that oogonia and antheridia are constituted by the ordinary vegetative segments and that numerous (often 100 or more) ova are formed in the oogonium. In both respects its sexual organs are directly comparable with those of an *Ulothrix* (or of one of the Cladophorales), whereas in Siphonales there are usually specially differentiated gametangia. The method of release of the male cells and of their admission to the female, through holes in the lateral walls, also recalls the state of affairs in *Ulothrix*. The annular chloroplasts so commonly found in *Sphaeroplea* are very similar to those of *Ulothrix zonata*. If in such a form as the latter no septa were to be produced over long intervals, we should obtain a condition practically identical with that found in *S. annulina*, etc., where, moreover, we get occasionally quite short "cells" with only one or two chloroplasts ((31) p. 20). In this and other species, again, the nuclei are practically confined to the regions of the chloroplasts, and there is sometimes only one nucleus to each ring. The facts point to the interpretation of each chloroplast with its associated nuclei as a single entity, the whole coenocyte consisting of a series of such entities, each of which may be directly compared with a single *Ulothrix*-cell.

The view just propounded that *Sphaeroplea* is derived from a septate Ulotrichaceous type which has ceased to form septa except at rare intervals—an advance that has gone hand in hand with the acquisition of a primitive type of oogamy—receives some further support from the fact that septation is apparently tending to disappear altogether in some species of the genus. Lastly, the mode of germination of the zygotes in *Sphaeroplea* is like that of *Ulothrix* and other haploid Green Algae, whilst the zygotes in the diploid Siphonales germinate direct.

A consideration of all these facts removes *Sphaeroplea* from the Siphonales, which it really only resembles in the coenocytic character of its segments, and brings it into close relation with the Ulotrichaceae. A form of great interest in this connection is furnished by the South African *Sphaeroplea tenuis* (fig. 67 F), about which unfortunately relatively little is as yet known (31). The narrow threads of this species very commonly exhibit empty segments provided with numerous and usually remarkably large circular holes (fig. 67 G), while others show preliminary stages in the formation of reproductive cells. No traces of oogonia are, however, to be found, and there is more than a suspicion that in this species both types of gametes are motile and liberated to the exterior. In the same material were found spores with an outer wall covered with spines, and many of these spores were found enclosed in a delicate smooth hyaline membrane, whilst others were lying just next to an empty membrane of this kind (fig. 67 M). In view of the similarity to what occurs in oospore-formation in the ordinary species of *Sphaeroplea*, there is some degree of likelihood that these spores may represent the zygotes of *S. tenuis*, since their size is of such an order that they might well have arisen from the fusion of gametes capable of escaping through the large apertures in the empty segments. There is some evidence, too, to indicate that, apart from the fact that both gametes are seemingly motile, they may not even be markedly dissimilar in size. A rediscovery of this species (which will probably be found to warrant the establishment of a distinct genus) in a more accessible habitat is much to be desired, since it may very probably prove to be an important connecting link between the normal species of *Sphaeroplea* and the isogamous Ulotrichaceae.

THE CLASSIFICATION OF ULOTRICHALES

It is only in the Ulotrichineae that there is sufficient diversity of type to warrant the establishment of distinct families. Here we may distinguish:

1. *Ulotrichaceae:* Binuclearia, Geminella, Gloeotila (?), Hormidium, Pearsoniella, Radiofilum, Schizomeris (?), Stichococcus, Ulothrix, Uronema (?).
2. *Microsporaceae:* Microspora.
3. *Cylindrocapsaceae:* Cylindrocapsa.
4. *Ulvaceae:* Enteromorpha, Letterstedtia, Monostroma, Ulva.

In the Prasiolineae and Sphaeropleineae, each with a single genus only, we have the families Prasiolaceae and Sphaeropleaceae.

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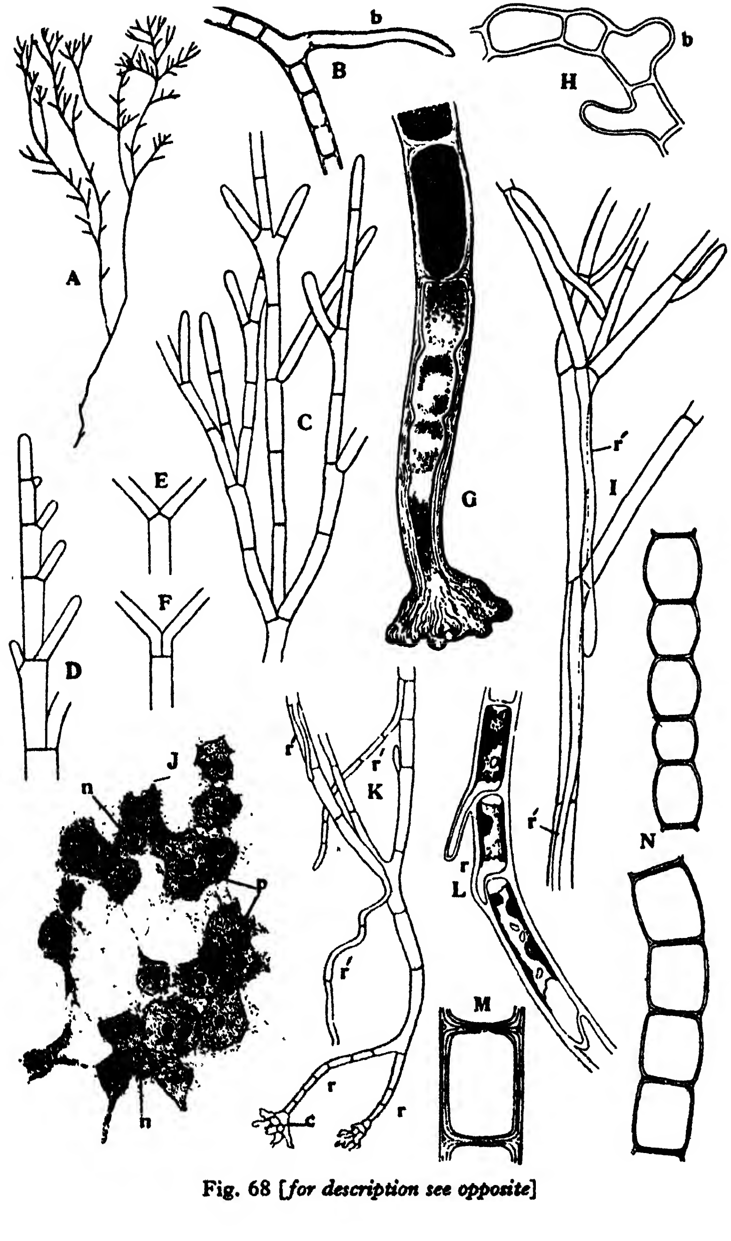

Fig. 68 [*for description see opposite*]

VEGETATIVE STRUCTURE

The Cladophoraceae are found both in freshwater and in the sea, where they inhabit mainly the rocks of the littoral zone; some, like the tropical *Pithophora*, are exclusively confined to freshwater, whilst others like *Urospora*[1] and *Spongomorpha* are found only in the sea or in brackish waters. *Rhizoclonium riparium* Harv. may occur on terrestrial substrata beyond reach of the sea (56), while it is commonly found on sand-covered rocks or even on pure sand, acting as a binder, as well as on salt-marshes ((21) p. 79). This preference for sandy pools is also shown by other members of the family (e.g. *Chaetomorpha aerea*). *Cladophora* (*Aegagropila*) *profunda* Brand (5, 77) is a widespread bottom-living form in many continental lakes where it is recorded as extending to depths of 24 metres. Members of the Cladophoraceae have occasionally been observed in symbiosis with sponges (40, 74).

The members of this family possess unbranched (*Urospora*, *Chaetomorpha*, fig. 68 N) or richly branched filaments (*Cladophora*, fig. 68 A, C; *Spongomorpha*, fig. 70 B), the cells of which are usually multinucleate and mostly elongate; short cells are frequent in *Chaetomorpha* (41) and *Urospora*. In some species of the latter there are short branches which are not cut off by a septum from the parent-cell (fig. 68 H). The threads of *Rhizoclonium* (7, 15, 28, 30, 68) are often altogether unbranched, though in other cases (commonly in the marine *R. riparium*) there are a number of very short, almost colourless, one- or few-celled branchlets of irregular shape which resemble, but do not function as rhizoids and are responsible for the generic name (fig. 68 B).

There is still much difference of opinion as regards the cell-structure. It is probable that the chloroplast is always fundamentally a single

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[1] *Hormiscia* Fries is a synonym.

Fig. 68. Vegetative structure of Cladophoraceae. A, C, *Cladophora glomerata* (L.) Kütz.; B, M, *Rhizoclonium hieroglyphicum* Kütz. var. *tortuosum* Stockm.; G, *Chaetomorpha aerea* Kütz.; H, *Urospora mirabilis* Aresch.; I, *Cladophora ophiophila* Magnus & Wille; J, *C. Suhriana* Kütz.; K, *C. glomerata* var. *simplicior* Brand; L, *Urospora elongata* (Rosenv.) Hagem; N, *Chaetomorpha Linum* (Müll.) Kütz. A, C, habit; B, H, branch-formation; D, diagram to explain evection; E, F, diagrams of dichotomy and basal fusion; G, growth of secondary rhizoids into the primary attaching cell; I, K, formation of rhizoids, in K the third rhizoid from the top emerges from the base of a branch which is about to be detached; J, part of chloroplast; L, cell-structure and rhizoid-formation; M, structure of cell-membrane. *b*, branch; *c*, cell-cluster arising from division of rhizoid; *n*, nucleus; *p*, pyrenoid; *r*, rhizoid. (A, B, M, N after West; C after Migula; G after Rosenvinge; H, L after Printz; I after Wille; J after Schussnig; the rest after Brand.)

structure, consisting of a parietal reticulum lodged in the cytoplasmic lining of the cell (fig. 69 A). This reticulum has meshes of very varied width and covers both the longitudinal and the transverse walls, frequently developing processes that extend inwards into the cytoplasmic strands traversing the large central vacuole (fig. 69 B). There are usually numerous scattered pyrenoids that multiply by division, although Printz (55) records small cells with a single pyrenoid in *Urospora mirabilis*. The preceding account is in brief the description of the chloroplast given by Carter ((17); cf. also (9) p. 517, (47)) and in cells that do not contain too much starch the reticulate distribution of the green pigment is readily recognisable.

More recent investigators on the continent (19, 64) have, however, maintained the older interpretation of Schmitz ((59) p. 15), according to which the mature reticulum is often composed of numerous separate, more or less readily distinguishable, discoid chloroplasts, some with and some without pyrenoids. According to Schussnig ((64) p. 482) there is a pyrenoid within each of these chloroplasts in *C. Suhriana* (fig. 68 J), whilst Czempyrek ((23) p. 436) states that in *C. callicoma* the pyrenoids are lodged in the granular ground matter *between* the chloroplasts; the last is probably a misinterpretation. In my opinion the nature of the Cladophoraceous chloroplast will never be clearly solved until it has been studied in young plants, where such evidence as is available would seem to indicate that it is a single structure (fig. 68 L) which may not even at first show much reticulation (cf. (55) p. 279). Obvious fragmentation of the chloroplast into many small pieces has not infrequently been observed in *Chaetomorpha* ((50) p. 97) and may no doubt occur at times in other genera.

The nuclei[1] are usually numerous and lie internal to or are embedded in the chloroplasts, often being distributed with great regularity. In the cells of *Rhizoclonium* the nuclei are mostly fewer, and both here (28, 53), as well as in *Cladophora* ((9) p. 519) and *Urospora* (55), there may sometimes be only one or two, while uninucleate cells certainly occur in some species of *Spongomorpha*.[2]

A marked characteristic is afforded by the thick clearly stratified membranes (fig. 68 M, 69 C), to which most Cladophoraceae owe their rough crisp feeling and probably their usual restriction to well-aerated waters (26); the chief exception in this respect is constituted by *Pithophora* (75), whose real home is indeed in somewhat stagnant tropical waters (26). In the thick walls an inner (*i*) and an outer (*o*) lamella, both usually clearly stratified (fig. 69 C, F), as well as a superficial pellicle (*l*) which can be separated by treatment with

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[1] With reference to structure and division of the nuclei of Cladophoraceae, see (17), (60), (64), (66). A rather divergent account is given by Nemec (49a).

[2] The species with multinucleate cells are often placed in a separate genus *Acrosiphonia*, but there seems to be little warrant for this (cf. (67) p. 221).

acetic acid, are distinguishable (9, 14); the inner lamella of the wall is individual to each cell. Both lamellae, when viewed from the surface, occasionally show a striation (13, 14) which generally runs obliquely and which, according to Correns (20), is due to folding of the individual strata. Very little, if any, mucilage is secreted by the cells of Cladophoraceae, and this is probably one of the main reasons why they are often loaded with epiphytes.

Where the threads are branched the branches nearly always arise

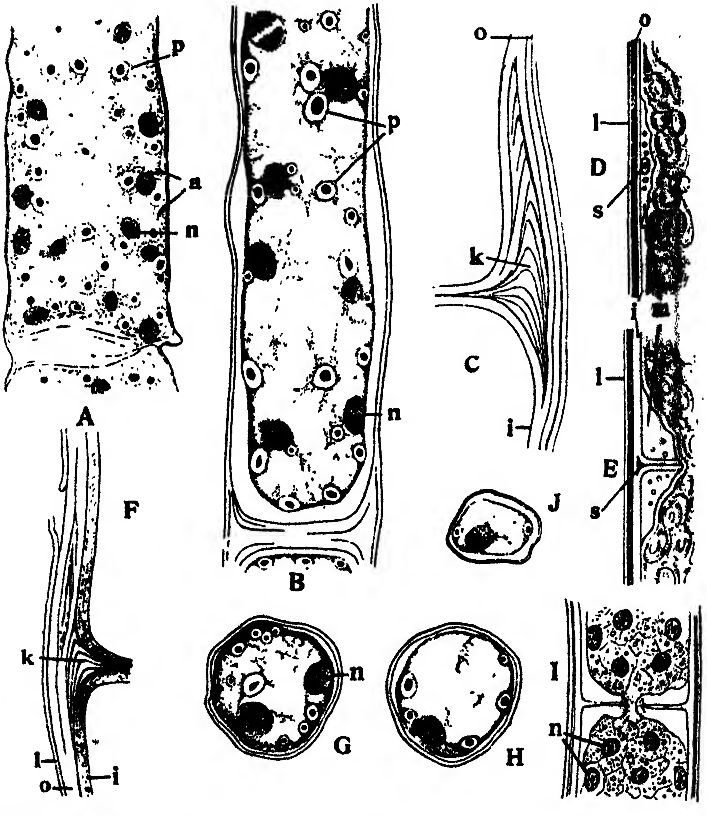

Fig. 69. Cell-structure of the Cladophoraceae. A, *Cladophora callicoma* Ag. B, G, H, J, *Rhizoclonium hieroglyphicum*; B, longitudinal section, the others transverse sections. C, F, *Cladophora glomerata*, structure of the membrane. D, E, I, the same, septum-formation. *a*, starch-grains; *i*, inner lamella of wall; *k*, joint; *l*, surface-lamella; *m*, mucilage; *n*, nucleus; *o*, outer lamella of wall; *p*, pyrenoid; *s*, septum. (C–F after Brand; I after Strasburger; the rest after Carter.)

from the upper end of the parent-cell, just beneath a septum (fig. 68 C). At first they form a wide angle with the main axis, the septum cutting off the branch being generally placed approximately perpendicular to those in the main axis. Sooner or later, however, by localised surface-growth of the membrane of the parent-cell beneath the branch, the latter becomes upwardly displaced (so-called *evection*, cf. fig. 68 D) and subsequently lies on the same level as the continuation of the main axis which often becomes pushed to one side (fig. 68 E), so that an appearance of dichotomy results ((9) p. 499, (8) p. 155). Not uncommonly two opposite branches are produced from either side of a parent-cell, so that with the subsequent changes a trichotomous appearance may be produced (fig. 68 C). In many cases, too, the inner lamella of the branch fuses basally with that of the next cell of the main axis (fig. 68 F), the outer lamella and superficial pellicle being pushed upwards and running continuously over the point of fusion (9, 51, 57).[1] All these phenomena are readily seen in species of *Cladophora*, although there are marked differences with respect to the rapidity with which evection and fusion of the bases of the branches takes place. In *Pithophora* the branches originate a little way beneath the septum, a condition also found in some of the aegagropilous *Cladophoras* (cf. p. 237). Mothes (48) has recorded a correlation between growth of the apical cell and development of laterals in the former genus.

In most genera of Cladophoraceae all the cells are capable of division, but in *Spongomorpha*, *Cladophora*, and *Pithophora* growth is partly carried out by the apical cells which, when they have reached a certain length, undergo division into two, the lower cell in many cases undergoing no further appreciable elongation ((2) p. 184, (24), (48)). In *Spongomorpha* and some *Cladophoras* there is abundant division in the segments cut off from the apical cell, while the aegagropilous species of the latter are stated to grow only apically ((10) p. 40). At the commencement of cell-division ((14), (69) p. 206) the protoplast withdraws from the wall along a transverse zone in the middle of the cell, the space (fig. 69 D, *m*) thus arising being probably occupied by mucilaginous matter. Within it is secreted an annular bar of thickening (fig. 69 D, *s*), the primordium of the septum, extending transversely round the cell; this is circular or oval in optical section and consists of a central core and an outer portion. In the further course of events the primordium grows centripetally inwards and, at the same time, extends into and fuses with the inner lamella of the longitudinal wall (fig. 69 E). The core of the original annular bar of thickening forms the middle lamella of the septum,

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[1] According to Cholnoky ((18) p. 556) such fusions are only found in threads producing akinetes and are a result of the pronounced thickening of the wall that takes place during this process.

whilst the outer part becomes continuous with the inner lamellae of the adjacent longitudinal walls (fig. 69 I). The formation of septa is not related in any way to nuclear division.

At an early stage the two lamellae of the septum separate from without inwards (14), whereby triangular spaces arise at the corners of the cells (fig. 69 C, F) which also gradually extend some little way upwards and downwards between the two lamellae of the longitudinal walls; these spaces are probably occupied by colourless pectic substances. In the older parts of the plants, and especially in the neighbourhood of the branches, these spaces contain folded lamellae (fig. 69 C, F, *k*), which seem to constitute joints contributing to the flexibility of the otherwise rather rigid threads; these joints have been studied in detail by Brand ((9) p. 492, (14)).

Except for the aegagropilous *Cladophoras* and *C. fracta*, the plants are primarily and often permanently attached to some substratum which is of course a necessary consequence of their frequent growth in moving waters (rivers, the littoral zones of lakes and the sea). In quiet waters, however, species of most genera can be found unattached, and everyone will be familiar with the floating tangles of *Cladophora* and *Rhizoclonium* met with in ponds. The basal attaching cells of *Chaetomorpha* are elongate, often possess a poorly developed chloroplast, and are usually broadened at the base which is commonly lobed (fig. 68 G). In *Cladophora* attachment is usually effected by a number of septate rhizoidal branches (fig. 68 K, *r*) arising from the base of the plant. These may sometimes spread out as stolons and give rise to new upright threads or their tips may divide into a number of short cells (cf. fig. 68 K; 70 E, *c*) which later fall apart and serve as a means of propagation and perennation (3, 11, 16, 29, 30). Origin of new threads from the attaching cells is also frequent in *Chaetomorpha* (3). Supplementary rhizoids which are thick-walled, narrow, and often multicellular, commonly originate from the lower ends of the cells above the basal one or even from the basal cells of the branches and, after reaching the substratum, aid in attachment as the plants grow larger (fig. 68 I, K, *r′*). These rhizoids may grow downwards through the strata of the thick walls or lie apposed to the basal cell or in some few cases may even stand off quite freely. They are specially developed in some of the marine *Cladophoras*, in *Urospora* ((27), (38), (55) p. 277) and in *Spongomorpha*. In *Chaetomorpha aerea* (fig. 68 G) the cell above the basal one may protrude into the latter and ultimately reach the substratum, and this may be followed by a similar outgrowth of successive overlying cells (57).

Peculiar tendril-like attaching organs (fig. 70 C, *h*) are to be found in most species of *Pithophora* (75). The tips of some of the ultimate branches become produced into narrow, usually branched and sometimes rhizoid-like outgrowths which possess green contents and are

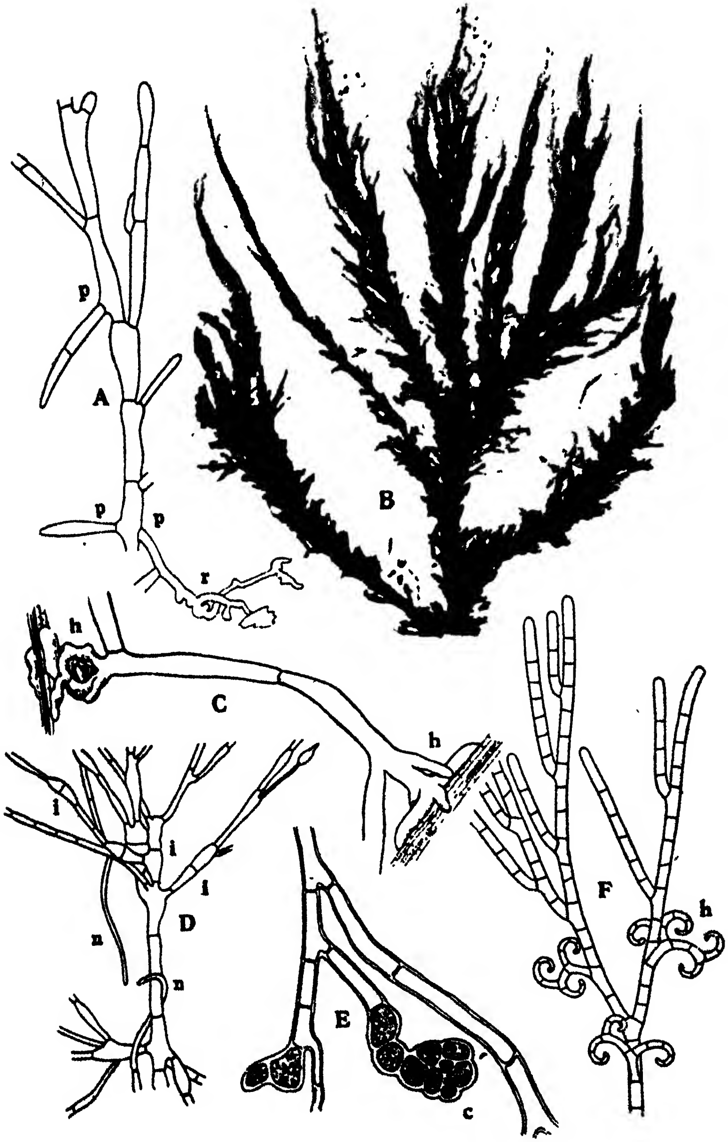

Fig. 70 [*for description see opposite*]

not cut off by a septum. These structures coil round foreign objects and thus aid in attachment.

THE AEGAGROPILOUS CLADOPHORACEAE

Somewhat similar structures are known to occur in the marine *Spongomorphas* and in those species of *Cladophora* commonly grouped in the genus *Aegagropila*, although it may be doubted whether they merit generic separation. In both cases the mature thalli are composed of more or less numerous individuals, as a rule probably originating from a single one by dying away of the older parts and setting free of the branches. The different individuals are held together by interlacing of the branches, some of which are developed as specially slender structures (the *neutral branches* of Brand (10)) which insinuate themselves between the others and are sometimes coiled round other branches at their tips (fig. 70 D, *n*, F). In the case of *Spongomorpha* (37) the diverse plants are connected to form dense bundles (fig. 70 B), but they do not constitute the thick growths found in the aegagropilous *Cladophoras*.[1] Here the individuals are associated in dense masses, appearing either as compact cushions attached to some substratum or sometimes as loose hollow balls which may become as big as a human head (fig. 70 *bis*, A). Such

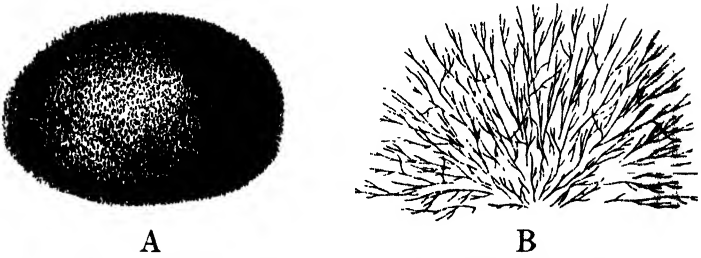

Fig. 70 *bis*. *Cladophora* (*Aegagropila*) *Sauteri* (Nees) Kütz. (after Lorenz). A, one of the balls about half natural size; B, part of a young attached growth.

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[1] See (1), (5), (10), (12), (39), (44), (45), (70).

Fig. 70. A, *Cladophora Martensii* Menegh., showing reversal of polarity at *p*, the lowest branch developing a rhizoid. B, F, *Spongomorpha coalita* (Rupr.) Collins; B, habit; F, branch-system with coiling laterals (*h*). C, *Pithophora affinis* Nordst., haptera (*h*). D, *Cladophora profunda* Brand, middle part of a bipolar plant, at *i* intercalary divisions are occurring. E, *Spongomorpha vernalis* (Kjellm.), rhizoids developing groups of storage-cells (*c*) at their tips. *n*, neutral filaments; *r*, rhizoids. (B, F after Setchell & Gardner; C after Moebius; E after Kjellman; the rest after Brand.)

growths are mainly found on the bottom of shallow lakes (6, 49), although similar marine types are also known (39, 76).

The plants in these cushions or balls are richly branched, in the main stand perpendicular to the surface (fig. 70 *bis*, B), and there is a progressive acropetal dying away of the innermost parts, whereby the branches become separate, although remaining bound together by the above-mentioned neutral filaments. In the attached growths the latter serve for fixation, but they can also grow out at their tips into normal shoots. According to Brand (10) the growth of the aegagropilous forms is altogether apical and very slow. The branches are commonly opposite and are not infrequently sharply bent. Moreover, complete inversion of polarity[1] is a common phenomenon, the branches in the lower part of the plant often growing in a direction opposite to that in the upper (fig. 70 A).

It seems clear that the attached cushions and the free balls are but different states of development, and the same species are also found growing in quiet water as swards of more or less independent plants (44, 70). The balls are only formed where the bottom is relatively firm and there is a gentle movement of the water leading to a constant rolling to and fro of detached masses of the alga. In the larger balls the structure is densest towards the surface, while the interior is much looser or even hollow, owing to the dying of the older parts and the tangential stretching due to the continual surface enlargement. The outer part commonly shows concentric darker and lighter zones, the latter composed of elongate cells with thin walls, the former of shorter cells with thick walls. It seems that the lighter zones are formed in summer, the others constituting the winter condition, so that two such zones may represent a year's growth (10, 45, 70). The aegagropilous growths have not inappropriately been compared to hedges, since projecting tips sooner or later die, but there is still difference of opinion whether the effect is a purely mechanical one or whether, as Brand (10) believed, projecting branches are destroyed by the stronger light to which they are exposed.

An aegagropilous growth has also been recorded in a species of *Chaetomorpha* (42), while Schiller (58) describes loose-lying communities composed of *Cladophora trichotoma* and species of *Chaetomorpha* from the Adriatic.

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[1] Such inversion of polarity can also occur in *Cladophora glomerata* (4, 22).

REPRODUCTION

Many, if not all, Cladophoraceae are perennial, but the mode of existence during periods unfavourable for growth varies in different forms. In *Spongomorpha* and in some species of *Cladophora* (cf. p. 235) the rhizoids, after reaching the substratum, commonly divide to form a cellular expanse (fig. 70 E) or in the latter genus a number of short branched filaments; their cells become filled with food-reserves and are sometimes encrusted with carbonate of lime. These structures persist after the remaining parts of the thalli have disappeared and give rise to new threads in the next season. In many of the freshwater forms a smaller or larger proportion of the cells of the ordinary threads become laden with food-reserves and undergo further thickening of their walls, commonly becoming more or less swollen and often assuming a pear-shaped form; in *Cladophora* it is mainly the larger branches that develop such dormant stages which are indeed often almost branchless (8, 30). This is a state of wholesale akinete-formation without dissociation of the threads. According to Cholnoky (18) the formation of such akinetes in *Cladophora glomerata* is preceded by repeated cell-division; when germination occurs, transverse division always takes place before branches are formed.

In *Pithophora* (fig. 71 A, A′) special akinetes are produced by the contraction of the greater part of the protoplasm of a cell towards one end (usually the upper) which becomes cut off by a septum and subsequently develops a thick wall (47, 75); in some cases these akinetes are formed in short series of two or three. Ernst (24) established that akinete-formation takes place when there is a deficiency of nutritive salts. According to Mothes (48) the remaining half of the mother-cell may, under cultural conditions, again become filled with protoplasm and may even occasionally form a second akinete, but it is not known whether this occurs in nature. Production of akinetes is the only method of reproduction known in *Pithophora*, apart from the vegetative propagation by detached branches which is probably of common occurrence in most Cladophoraceae. In the aegagropilous *Cladophoras* (10) there appears to be only vegetative propagation.[1]

In all the other genera asexual reproduction is effected by zoospores. These arise by simultaneous division of the cell-contents into numerous small parts (fig. 71 B) which is preceded by a gradual encroachment of the protoplasm on the central vacuole and abundant nuclear division ((64) p. 481). In *Cladophora* such swarmer-formation appears normally to be confined to the finer branches and often takes place in definite basipetal succession, but in the other genera any cell may apparently form zoospores except for the basal attaching cell. The

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[1] Nishimura and Kanno (50) record biflagellate swarmers in *Cladophora* (*Aegagropila*) *Sauteri*, but this requires confirmation.

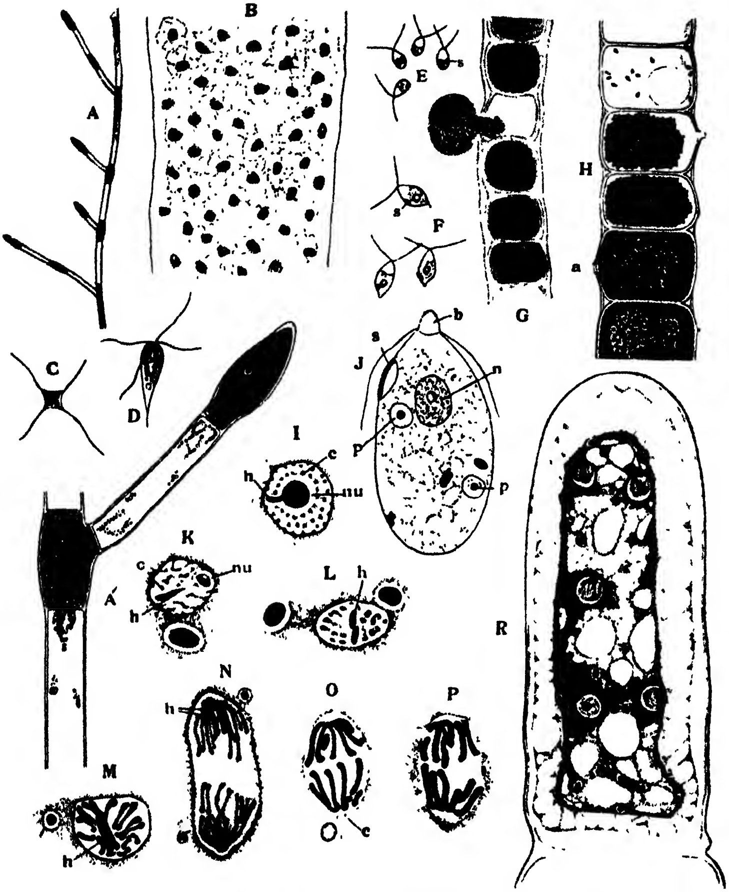

Fig. 71. Reproduction of the Cladophoraceae. A, A′, *Pithophora kewensis* Wittr., akinete-formation. B, *Cladophora glomerata* (L.) Kütz., delimitation of zoospores. C, D, *Urospora penicilliformis* (Roth) Aresch., zoospores in front- (C) and side-views (D). E–G, *U. mirabilis* Aresch.; E, male, and F, female gametes; G, thread with male gametangia, one dehiscing. H, *Chaetomorpha aerea* Kütz., thread producing zoospores. I, K–P, R, *Cladophora Suhriana* Kütz. I, K–M, somatic mitosis in the sporophyte; I, resting nucleus; K, early prophase; L, division of heterochromosome; M, metaphase, longitudinal division of chromosomes. N, heterotypic mitosis, telophase. O, P, mitosis in the gametophyte, with seven and six chromosomes respectively; R, sporangial cell, nuclei in synapsis. J, *Cladophora* sp., gamete. *a*, aperture of gametangium; *b*, beak of swarmer; *c*, centrosome; *h*, heterochromosome; *n*, nucleus; *nu*, nucleolus; *p*, pyrenoid; *s*, stigma. (A, A′ after Wittrock; B after Czempyrek; C, D after Areschoug; E–G after Printz; H after Thuret; J after Strasburger; the rest after Schussnig.)

details have been described by Czempyrek (23) and Schussnig (64) for *Cladophora*.[1] According to them the swarmers are not formed by cleavage, but by a gradual aggregation of the cytoplasm around the nuclei. In some species of *Urospora* (55) the zoospores exhibit a radial arrangement with the anterior extremities outwards. There is no disappearance of pyrenoids during swarmer-formation.

In most cases the zoospores are pear-shaped and quadriflagellate, but in certain species of *Cladophora* (*C. glomerata* (43, 61); *C. Suhriana* ((64) p. 479)) and *Rhizoclonium* they are known to be biflagellate; according to Wille (72) the two flagella are unequal in some species of *Rhizoclonium*. The zoospores of *Urospora* (27, 31) are obovate and produced into a long point at their posterior end (fig. 71 C, D), while from the front they appear quadrangular, although the outline is variable owing to slight changes of shape. In all cases the swarmers are liberated through a lateral aperture in the wall (fig. 71 G, H).

Biflagellate gametes are known in *Chaetomorpha*, *Urospora*, and *Cladophora* (fig. 71 J) and are formed and liberated in the same way as the zoospores. They are usually isogamous, but *Urospora* (55) produces small almost colourless male gametes and larger female gametes with a chloroplast containing a prominent pyrenoid; both have an almost posterior stigma (fig. 71 E, F). The threads producing the male gametes early acquire a pale appearance owing to the gradual disappearance of chloroplasts and pyrenoids. A similar heterogamy is reported by Hamel (32) in *Rhizoclonium lubricum* Setchell and Gardner which they regard as the type of a new genus (*Lola*). The zygotes of *Cladophora* germinate directly, those of *Chaetomorpha* after a few days ((33) p. 486), while those of *Urospora* according to Jorde (78) develop into *Codiolum*-like stages which multiply by zoospores. In the other cases the germination is direct.

There can be little doubt that most of the sexually reproducing Cladophoraceae normally exhibit an homologous (isomorphic) alternation between asexual and sexual individuals, although this has so far only been certainly established in some species of *Cladophora* (25, 61, 62) and *Chaetomorpha* (33). There are some indications, too, that in certain regions (e.g. the Mediterranean) the two generations may be seasonally segregated ((64) p. 480). In both the genera mentioned fusion only occurs between gametes from distinct strains, so that these forms are dioecious. It has been established by Schussnig (61) in a number of species of *Cladophora* that reduction occurs during the nuclear divisions leading to the formation of zoospores (cf. fig. 71 R). In the case of *C. Suhriana* (63, 64) and *C. flexicaulis* (65) the same investigator recognises, during the early phases of the heterotype division, an extra chromosome (heterochromosome) which is usually markedly elongate in form and is distributed to only one of

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[1] The account given by Colmant (19) differs in certain particulars.

the resulting daughter-nuclei (cf. fig. 71 N), so that equal numbers of zoospores with and without the accessory chromosome are produced. This chromosome has also been recognised in the ordinary vegetative divisions of the diploid individuals (cf. fig. 71 K–M, *h*), and it is suggested that its presence in only some of the haploid plants resulting from the germination of the zoospores (cf. fig. 71 O with 71 P) may be related to the dioecism of the latter. Neither in *C. glomerata* (43), nor in *C. flavescens* (34), however, has such an accessory chromosome been observed (cf. also (64) p. 521). In *Urospora* (78) the diploid phase is presumably constituted by the *Codiolum*-stage.

The recent investigation of *Cladophora glomerata* by List ((43); cf. also (60)) has, however, displayed an altogether different type of life-history. In this species zoospore-formation takes place at intervals all through the year, while gametes are only formed in spring at the end of a longer period of zoospore-formation. The zoospores and gametes are produced on distinct individuals, but there is no reduction of chromosome-number in the production of the former, while it is during the formation of gametes that reduction occurs. Certain peculiarities in the formation of chromosomes and in their mode of separation were, however, noted in the first nuclear divisions leading to the formation of zoospores. *C. glomerata* is therefore purely diploid, except for the gametes, and in this respect resembles the Siphonales. The diploid plants, however, evidently propagate by a long succession of diploid zoospores and the cause of the formation of the purely sexual plants found in spring is not clear. Higgins (35), in the case of *C. flavescens*, records very occasional fusions between the swarmers liberated from the sporangia in which she had demonstrated a reduction division and suggests that this may be due to the haploid zoospores possessing some sexual potentialities. In view of the state of affairs existing in *C. glomerata*, however, it is possible that *C. flavescens* may prove to be another diploid species.

Parthenogenesis has been recorded in *Chaetomorpha* ((33) p. 489) and *Cladophora* ((25) p. 500).

THE AFFINITIES OF THE CLADOPHORACEAE

The Cladophoraceae show resemblances to the Ulotrichales in the formation of the reproductive elements in unmodified cells, whereas in the majority of the Siphonales there are specialised sporangia or gametangia. Quadriflagellate swarmers, which are frequent in Cladophoraceae, are unknown in the Siphonales. The mode of liberation of the swarmers, through a lateral aperture, also recalls the state of affairs in Ulotrichales. The fact that the chloroplast is fundamentally single and readily derivable from a parietal plate and the occasional occurrence of cells with a single nucleus constitute further points of resemblance, the elaboration of the former and the frequent large numbers of the latter appearing as special differentiations resulting from the large size of the cells. By contrast to the Valoniaceae[1] (p. 413), moreover, with which the Cladophoraceae are usually associated, the filamentous habit is assumed immediately on germination, whereas in the former family the early stages are vesicular and more or less like a *Valonia*, the filamentous habit arising later and in a manner quite different from that found in the Cladophoraceae (segregative division, p. 415).

For these diverse reasons it is probable that there is no close relation between Cladophoraceae and the true Siphonales and that the former are an offshoot from the evolutionary series represented by the Ulotrichales. It is significant in this connection that there is an advance to homologous alternation. A coenocytic tendency is not uncommon among Chlorococcales and it would not be surprising if such a tendency likewise existed in some of the filamentous forms arising from the unicellular ancestry. Schussnig ((64) p. 512) draws attention to certain features in which the swarmers of *Cladophora* resemble those of Siphonales and differ from those of Ulotrichales, but it is scarcely at present possible to evaluate the nature of these differences.

THE GENUS *WITTROCKIELLA*

This genus, with a single species (*W. paradoxa* Wille (73)), is the only representative of the family Wittrockiellaceae whose affinities are difficult to determine. The alga in question grows on the earth amid various Myxophyceae in the neighbourhood of brackish marshes and is as yet only reported from Norway and North America.[2] It consists of short little branched upright threads (fig. 72 A), which form a thin brownish stratum on the earth. The threads are covered with a tough mucilage produced from the outer layers of the thick cell-walls, the upper cells being spherical or oval, while the lower ones are narrower and more elongate. Downwardly growing branches develop into multicellular rhizoids (fig. 72 B, *r*).

The cell-structure is altogether Cladophoraceous, the cells containing a reticulate chloroplast with numerous pyrenoids and several nuclei (fig. 72 D). The upper cells harbour numerous yellow oil-drops (haematochrome?) that give them an orange-coloured appearance, while similar drops found in the lower cells are green-coloured. The older cell-walls are very thick and prominently stratified. The uppermost cell of each thread bears a colourless hair which is cut off by a

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[1] Including the Siphonocladiaceae of others.

[2] According to Printz ((54) p. 227).

septum and may attain appreciable length; these hairs are outgrowths of the inner layers of the wall and the ruptured outer layers form a kind of sheath round the base (fig. 72 C, *s*).

Akinetes are formed from the uppermost cells of the threads (fig. 72 F), while sporangia producing a considerable number of aplanospores

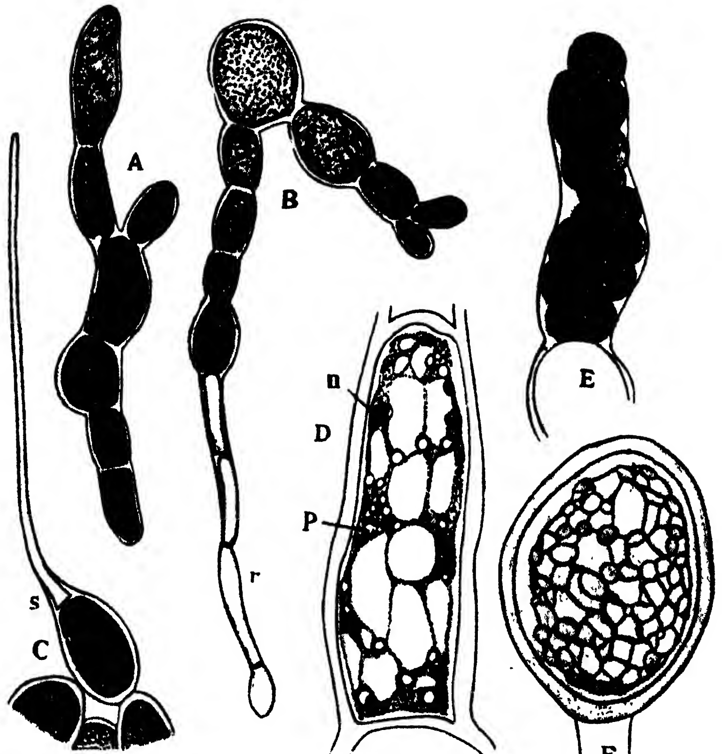

Fig. 72. *Wittrockiella paradoxa* Wille (after Wille). A and B, two plants, that in B with a downwardly growing branch terminating in a rhizoid (*r*); C, apex of a plant bearing a hair; D, single cell; E, sporangium with aplanospores; F, akinete. *n*, nucleus; *p*, pyrenoid; *s*, sheath of hair.

(fig. 72 E) arise from the cells below those bearing the hairs. No other methods of reproduction are known.

This genus combines characteristics of Cladophoraceae, Chaetophoraceae, and Trentepohliaceae. It resembles the last in the formation of special sporangia and in the probable presence of haematochrome in the cells, while the termination of the branches in hairs recalls

Chaetophoraceae, although the hairs are of a rather different type. The most marked affinities, however, appear to be with the Cladophoraceae. The apparent absence of a prostrate system is not in favour of a close relationship with the Chaetophorales, while the presence of haematochrome is perhaps but a result of the terrestrial habitat. *Wittrockiella* affords further support for the view that the multinucleate character of the Cladophoraceous cell cannot be taken as implying any affinity with Siphonales.

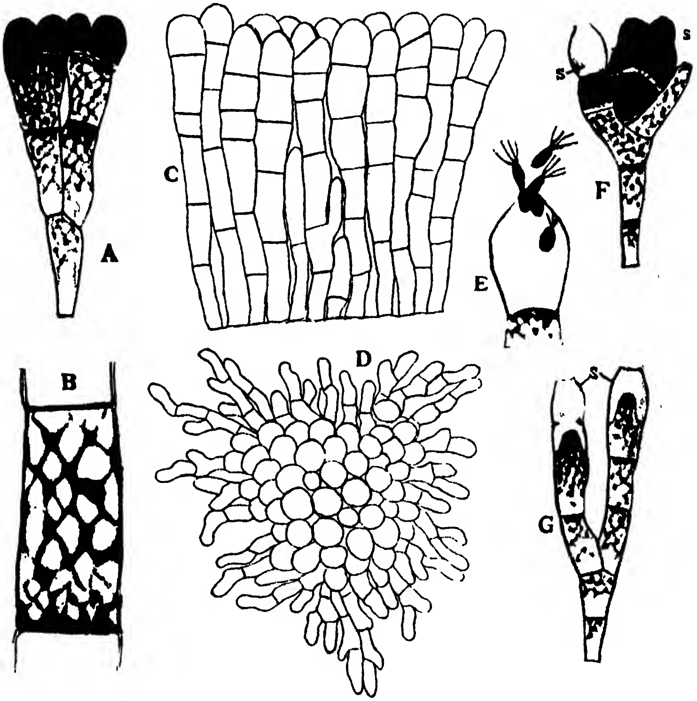

Fig. 73. *Arnoldiella conchophila* Miller (after Miller). A, one of the upright threads; B, single cell; C, section of a crust; D, the prostrate system; E, escape of zoospores; F and G, threads with apical sporangia (*s*), in part dehisced.

THE GENUS *ARNOLDIELLA*

This interesting member of the Cladophorales was found by Miller (46) forming dark green crusts on the surface of the shells of *Anodonta* and *Unio* in a lake in Central Russia. It is of special note because the filaments are heterotrichous (cf. p. 20), consisting of a basal one-layered creeping stratum formed by coalescence of prostrate threads (fig. 73 D) from which densely apposed and little branched, short, upright threads arise (fig. 73 A, C). The basal stratum is apparently rarely composed of a single plant, but usually results from the coalescence of a number. The cells show typical Cladophoraceous structure (fig. 73 B).

Reproduction is effected by quadriflagellate zoospores which are formed in large numbers in terminal sporangia (fig. 73 F, *s*) and are liberated through an apical pore (fig. 73 E). Formation of akinetes rich in starch was also observed.

In its heterotrichous habit this form is so different from other Cladophorales that it should no doubt be referred to a distinct family, Arnoldiellaceae. There is, however, some affinity with Cladophoraceae as evidenced by the cell-structure and the swarmers.

Hoffmann and Tilden (36) have described a genus, *Basicladia*, not uncommon on the carapace of turtles on the American continent, which likewise appears to possess a heterotrichous habit, the little branched erect filaments being described as arising from creeping rhizome-like threads fastened by holdfasts having free or coalesced branches.

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Order V. *CHAETOPHORALES*

There is a fundamental difference between the organisation of the Chaetophorales and that of the Ulotrichales, evident enough in the more typical representatives of the families Chaetophoraceae, Trentepohliaceae, and Coleochaetaceae, but obscured or almost unrecognisable in the numerous specialised forms that belong to this order. This outstanding characteristic lies in the differentiation of the vegetative body (cf. fig. 74 A) into a prostrate system of branching threads (*b*) attached to some substratum and a projecting system (*e*) likewise composed of branching filaments ((8) p. 139, (43)), in short the type of plant-body known as the heterotrichous filament (46) and widely distributed also in other classes of Algae. The two parts of the thallus are easily distinguished in many species of *Stigeoclonium* (fig. 74 A), *Gongrosira*, *Trentepohlia* (fig. 84 A), and *Coleochaete*, whilst a reduction of the projecting system has given rise to numerous prostrate and discoid types. In the Ulotrichales, on the other hand, no such differentiation exists and prostrate types are unknown, and this is equally true of the Cladophorales, except for the genera *Arnoldiella* and *Basicladia*, whose affinities are unclear. In the possession of the heterotrichous habit the Chaetophorales are to be regarded as the most highly differentiated forms among Green Algae.

In other respects, too, the Chaetophorales betray a high development, as for instance in the advanced differentiation of the threads in *Draparnaldia* (fig. 75 D) and *Draparnaldiopsis* (frontispiece), in the specialised oogamy accompanied by a kind of "fruit" formation in *Coleochaete*, in the high degree of adaptation of the *Trentepohlias* to a terrestrial existence, etc. In no other order of the Chlorophyceae do we find such a diversity of growth-forms. It is not improbable that the Chaetophorales represent the surviving descendants of forms from which the higher plants arose in the remote past (43, 46).

The principal characteristic of the Chaetophorales is not implied in the name which refers to the formation of "hairs". Under this designation, however, are comprised at least two perfectly distinct kinds of structures. In the Chaetophoraceae the hairs are single elongated cells or rows of narrow elongated cells with scanty colourless contents (figs. 74 B and 75 B, *h*), whereas in the Coleochaetaceae and Chaetosphaeridiaceae they are outgrowths of the wall (bristles or setae, fig. 87 E, *h*) (66, 98). In the European Trentepohliaceae and in certain representatives of the other families hairs are, moreover, altogether lacking. Further, similar structures are commonly found in heterotrichous types among Phaeophyceae and Rhodophyceae. It will be quite apparent, therefore, that the production of hairs cannot be regarded as a distinctive feature of the order and one may well be going astray in including certain simple seta-bearing forms (Chaetosphaeridiaceae, p. 286) in the same group with the others. It is, however, impossible to gauge how far the process of reduction has gone within the Chaetophorales.

(*a*) THE FAMILY CHAETOPHORACEAE

The Chaetophoreae

An affinity of the less specialised members of this family with the Ulotrichaceae is plainly recognisable, both in the cell-structure and in the reproductive features ((112) p. 55), and a common origin for the two sets of forms along divergent lines is not improbable. The fila-

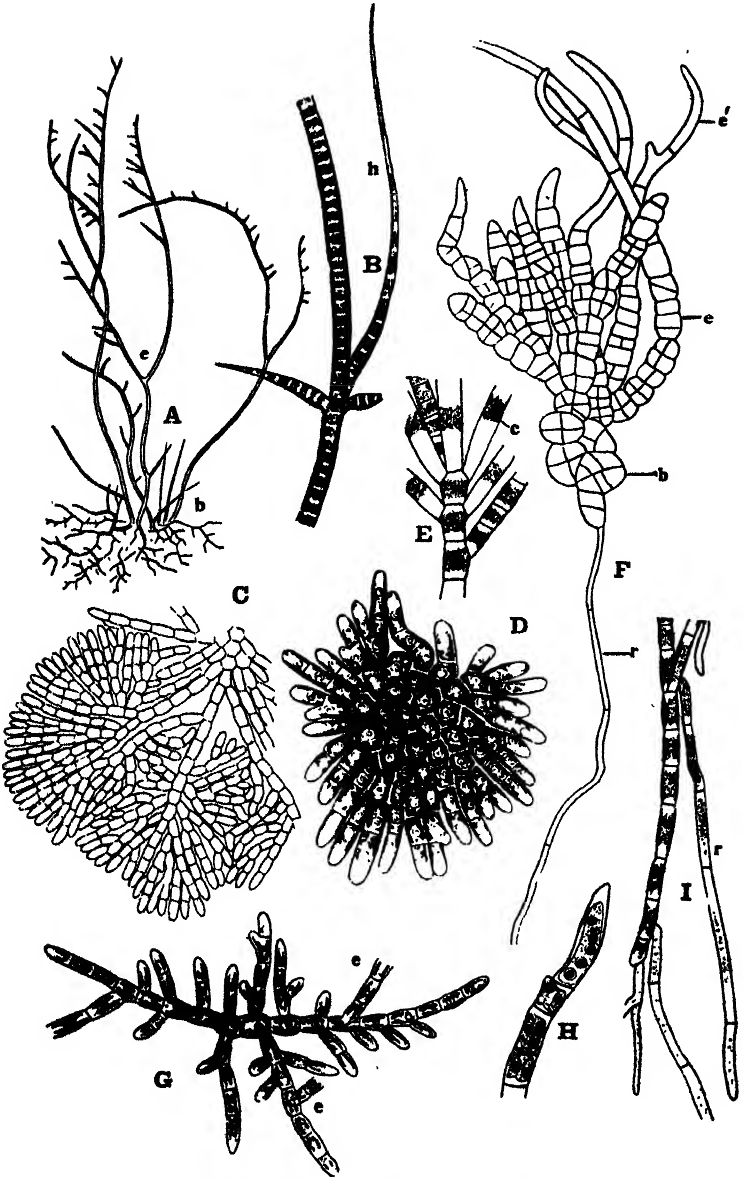

Fig. 74 [*for description see opposite*]

mentous Chaetophorales are, however, practically always branched.[1] The central type is constituted by *Stigeoclonium* (*Myxonema*),[2] in many "species" of which both prostrate and projecting systems are well developed (cf. fig. 74 A). Each cell, except those forming the hairs, contains a single parietal girdle-shaped chloroplast with one or more pyrenoids (fig. 74 E, I), often occupying only part of the length of the cell.

The projecting threads are usually well branched, the diverse branches terminating in a point or in long hyaline hairs (fig. 74 B). The branches arise from the top of the parent-cell and evection (p. 234) is frequent. Klebs (79) found that the extent of branching depended on the intensity of illumination, whilst Vischer ((152a) p. 45) has established that an abundant supply of nutritive salts is most essential, light determining the orientation of the branch. Hairs are produced much more plentifully in standing than in flowing water (cf. also (152a) p. 48). The consequent variability in the appearance of the projecting threads in this and other genera of Chaetophoraceae renders specific distinction a matter of great difficulty, and a determination of the range of variation of the diverse forms in nature is urgently required. The projecting threads of adult plants are frequently detached from the base and found floating freely in ponds and ditches.

Since the prostrate system accommodates itself to all the irregularities of the substratum, it is not easily detached or studied, and is therefore in the majority of cases very incompletely known. By contrast with the projecting threads in which there is usually no localised cell-division,[3] those forming the prostrate system (fig. 74 C, D) exhibit apical growth and are generally composed of shorter cells. The differentiation of the prostrate system ranges from a loosely branched thread composed often of relatively few cells (fig. 74 A, G) to a richly branched expanse (fig. 74 C) or a compact disc built up of

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[1] It is of interest in this connection that Gross ((54) p. 214; cf. also (88)) records the formation of branched threads in old cultures of *Ulothrix*. These recall in some measure the branching of a *Stigeoclonium*.

[2] See (6), (21), (28), (79).

[3] Vischer ((152a) p. 58) describes a similar form under the name of *Caespitella*, which is stated to have apical growth, although the evidence of its occurrence is not altogether convincing.

Fig. 74. A, *Stigeoclonium tenue* Rabenh., habit. B, *S. protensum* Kütz., part of an erect thread. C, D, *S. farctum* Berth., prostrate system; D, a young stage. E, *S. amoenum* Kütz., part of an erect thread. F, H, *Fritschiella tuberosa* Iyeng.; H, branch of projecting system. G, *Stigeoclonium lubricum* (Dillw.) Kütz., part of prostrate system. I, *S. aestivale* (Hazen), rhizoid-formation. *b*, prostrate system; *c*, chloroplast; *e*, projecting system; *e′*, secondary projecting system; *h*, hair; *r*, rhizoid. (A after Huber; B after Thuret; E, I after Hazen; F, H after Iyengar; the rest after Berthold.)

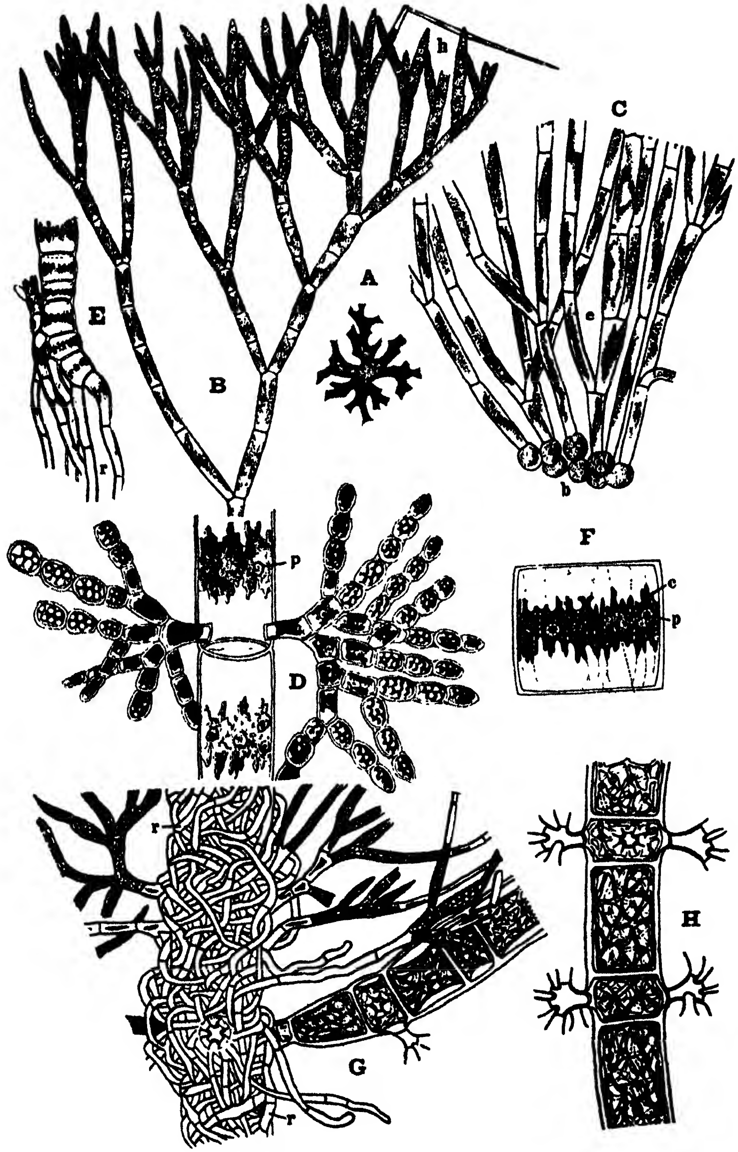

Fig. 75 [*for description see opposite*]

numerous branches coalescent to form a one-layered stratum (e.g. *S. farctum* Berthold (6, 40)) (fig. 74 D), in which the free ends of the branches may or may not project peripherally. In general it seems that the development of the projecting system is in inverse ratio to that of the prostrate one, but how far this ratio may be subject to variation in one and the same species in different habitats is not known. In forms with an elaborate prostrate disc the upright system may be reduced to a few short branches or in places be only represented by hairs ((44) p. 531).[1] Where the base is poorly developed the lower cells of the erect threads often put out rhizoids (fig. 74 I, *r*) which aid in attachment. *Pilinia* (30) (*Acroblaste* Reinsch (127)), a marine genus in which the chloroplasts lack pyrenoids (fig. 76 K), shows the same differentiation as *Stigeoclonium*, the threads of the upright system being sparsely branched.

Two interesting terrestrial allies of *Stigeoclonium* are known. *Iwanoffia* (71, 109) has quite the habit of this genus, the prostrate system creeping on the soil and being anchored by rhizoids. *Fritschiella* (72) has a higher differentiation (fig. 74 F), the prostrate system, more or less buried in damp mud, consisting of rounded clusters of cells (*b*) which appear to constitute the means of perennation, while the projecting system is differentiated into two regions (*e*, *e'*).

There is usually little difference between the width of the successive branches in the projecting threads of a *Stigeoclonium*, but in some (e.g. *S. amoenum* Kütz., fig. 74 E) the main axes contrast with the finer branches in the possession of thick-walled elongated cells with a meagre chloroplast, those bearing branches being shorter than the others (60). This is a step in the direction of *Draparnaldia* (6, 60), in which the prostrate system is usually practically absent, while the projecting part is strikingly differentiated into long and short branches (fig. 75 D). The long axes consist of large, often slightly barrel-shaped cells with a small chloroplast, having deeply incised edges and several pyrenoids (*p*) and often forming merely an equatorial girdle in the cell (fig. 75 F). The short laterals arise in dense, frequently more or less whorled tufts, are richly branched and composed of short cells

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[1] A similar type is seen in *Endoclonium* ((38), (67) p. 270, (146)), an epiphyte or endophyte in *Lemna*, which is now usually regarded as a reduced species of *Stigeoclonium* developing few or no upright threads.

Fig. 75. A, *Chaetophora incrassata* (Huds.) Hazen, habit (after West). B, C, *C. elegans* (Roth) Ag. (after Hazen); B, one of the radiating threads; C, basal system and uprising threads. D, *Draparnaldia glomerata* (Vauch.) Ag. (after Gay), hypnospore-formation. E, *D. plumosa* (Vauch.) Ag. (after Berthold), rhizoid-formation. F, *D. glomerata* (after Schmitz), cell of main axis. G, H, *Draparnaldiopsis indica* Bharad. (after Bharadwaja); G, rhizoidal cortex; H, main axis with bases of four laterals. *b*, basal system; *c*, chloroplast; *e*, projecting system; *h*, hair; *p*, pyrenoid; *r*, rhizoid.

occupied by a large generally entire chloroplast similar to that of *Stigeoclonium*; the apices of these branches frequently taper into long hyaline hairs and cell-division is apparently often confined to a few underlying cells (6). Attachment is effected by the reduced basal system, supplemented by multicellular rhizoids originating from the cells above (fig. 75 E). The development of reproductive cells, and no doubt also the chief assimilatory activity, are restricted to the short branches, the long ones fulfilling in the main only a supporting function. The contrast between the two types of branches is, however, not always pronounced, in fact one occasionally finds specimens in which the main axes are scarcely distinguishable. According to Uspenskaja ((151); cf. also (145 *a*)) these *Stigeoclonium*-like forms occur in habitats rich in nitrogenous matter and can be reared artificially in culture-solutions containing an excess of nitrates.

A further advance is seen in *Draparnaldiopsis* (7, 141), in which the long axes are composed of long and short cells, the latter alone bearing the laterals of limited and unlimited growth, commonly in whorls of four (fig. 75 H; cf. also frontispiece). In *D. indica* there is a great tendency for the transformation of branches of these short laterals into rhizoid-like structures and, especially at the points where laterals of unlimited growth arise, the production of such rhizoids may be very prolific; here they coil around the main axis and may branch so profusely as to form a dense cortical investment around the latter (fig. 75 G). The formation of a somewhat similar rhizoidal investment is recorded by Berthold ((6); cf. also (55)) in *Draparnaldia glomerata* and striking instances are described by Meyer (94) in *D. baicalensis* and *D. villosa*, where the whole of the lower part of the long axes is enshrouded to a thickness considerably exceeding that of the axis itself. In no other Green Algae is there so high a degree of differentiation as in these species of *Draparnaldia* and *Draparnaldiopsis*.

In *Stigeoclonium* and *Draparnaldia* the threads are commonly embedded in thin mucilage, but in *Chaetophora* (6, 60) they are held together within a compact mucilage-envelope to form large and conspicuous structures which are either more or less globose or foliaceous and branched (fig. 75 A); in some cases they are encrusted with lime (149). The prostrate system is feebly developed and often consists only of loosely connected rounded cells (fig. 75 C, *b*); from these the filaments of the projecting system (*e*) radiate out, at first branching but little, but later bearing dense clusters of bright green branches, the ends as usual often prolonged into hairs, beneath which an intercalary meristem may be located (fig. 75 B). The inner cells of the aggregate often have a poorly developed chloroplast, whilst rhizoids not uncommonly arise from some of the cells of older plants.

REPRODUCTION OF THE CHAETOPHOREAE

The genera discussed in the preceding pages form a connected group which may be classed as Chaetophoreae. Their reproduction[1] has been most fully studied in *Stigeoclonium*, *Draparnaldia*, and *Chaetophora*, in all of which both asexual and sexual propagation accomplished by means of motile swarmers has been recorded. It would seem that in the majority of the Chaetophoreae only two types of swarmers are produced, viz. (*a*) large invariably asexual macrozoospores (fig. 76 C), quadriflagellate in all but *Iwanoffia* (fig. 76 L) and *Pilinia*, and (*b*) smaller microzoospores which are quadriflagellate in *Stigeoclonium* (fig. 76 H) and *Draparnaldia* (fig. 76 E, F), but biflagellate in other cases. The smaller swarmers seem for the most part to be of the nature of gametes, and a fusion between them has been observed in species of most genera (cf. fig. 76 I), but they are also known to be capable of forming thick-walled resting stages[2] without fusion or in rare cases of growing out direct into a new plant. It is noticeable that Klebs ((79) p. 410) never observed fusion between the microzoospores of the form of *Stigeoclonium* that he studied. These facts may either imply a tendency towards parthenogenesis or may indicate the existence of a special type of microzoospore, not readily distinguishable from the gamete.

The two kinds of swarmers not only differ in size, but the microzoospores are of more slender build and have a projecting stigma (fig. 76 H) by contrast to the flat stigma of the macrozoospores. The former, moreover, exhibit a longer period of movement and a greater sensitiveness to light (79, 112), in all these respects resembling the microzoospores of *Ulothrix* (p. 203). According to Uspenskaja (151) the formation of the two types of swarmers in *Draparnaldia glomerata* is determined by the hydrogen-ion concentration of the medium, microzoospore-formation being induced by marked alkalinity.

In two of the four species of *Stigeoclonium* studied by Pascher (112) (*S. longipilum*, *S. fasciculare*) a third type of swarmer (invariably biflagellate) was observed, recalling in its morphological features the gametes of *Ulothrix*, so that in these species, which are vegetatively little specialised, we have the same three types of swarmers as in the latter genus; the biflagellate swarmers are not, however, formed in any numbers and sexual fusion is apparently exceedingly rare. Pascher is of the opinion that the sexual rôle fulfilled in *Ulothrix* by the biflagellate swarmer has been taken over in *Stigeoclonium* and *Draparnaldia* (108) by the quadriflagellate microzoospore with the complete elimination of the biflagellate type, except in the two species of the former genus above mentioned. On the other hand in *Chaetophora* (112) and *Endo-*

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[1] See (48), (74), (79), (102), (109–112), (148).

[2] Such hypnospores may be formed direct within the mother-cell without a previous period of swarming (fig. 76 D).

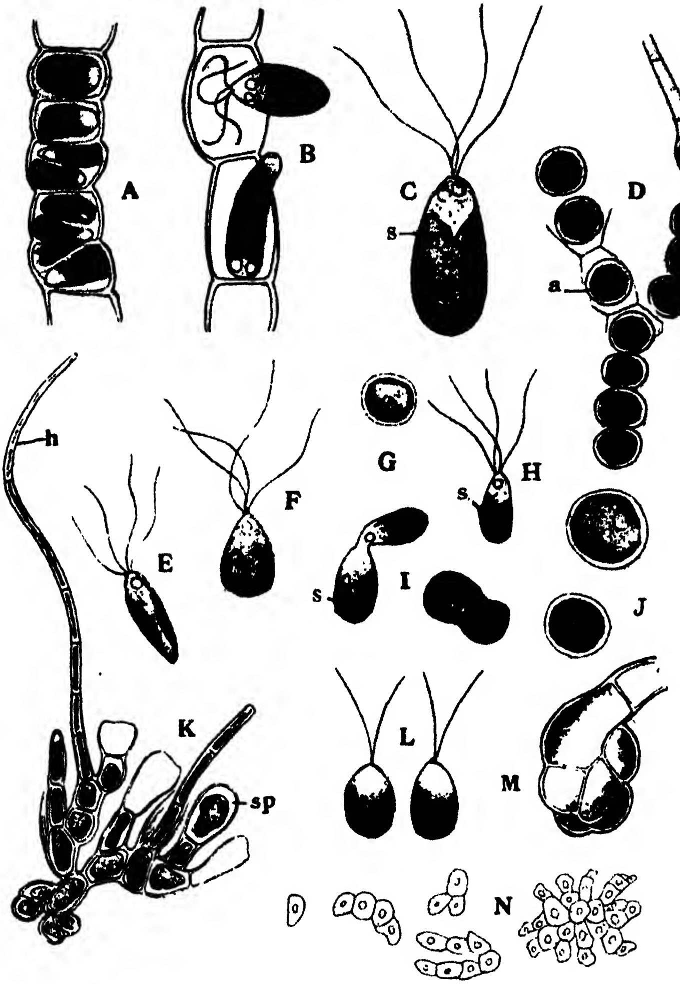

Fig. 76. Reproduction of the Chaetophoreae. A, B, H, M, *Stigeoclonium tenue* Kütz.; C–G I, J, *Draparnaldia glomerata*; K, *Pilinia maritima* (Kjell.) Rosenv.; L, *Iwanoffia terrestris* (Iwanoff) Pascher; N, *Stigeoclonium farctum* var. *simplex* Fritsch. A, formation of zoospores; B, escape of same; C, macrozoospore; D, formation of hypnospores (*a*); E, F, H, microzoospores; G, J, zygotes; I, fusion of microzoospores; K, branch of *Pilinia* with sporangia (*sp*), in part dehisced; L, swarmer of *Iwanoffia*; M, germling from a hypnospore; N, stages in development of prostrate system; *s*, eye-spot. (K after Rosenvinge; L after Iwanoff; N after Fritsch; the rest after Klebs.)

clonium (38) no quadriflagellate microzoospores are known, and in the former it is the biflagellate swarmer that functions as a gamete. In *Endoclonium* these swarmers, which penetrate through the stomata into the interior of the host (*Lemna*), can form hypnospores without fusion, these resting stages subsequently producing biflagellate zoospores which give rise to the ordinary threads. As opposed to this prevalently tetrakontan series of forms, we have the dikontan series represented by *Pilinia* and *Iwanoffia* (fig. 76 L), in which sexual fusion has not yet been observed, although the latter genus produces both macro- and micro-zoospores, either type with two flagella (cf. the dikontan *Hormidium* among Ulotrichaceae).

Pascher specially draws attention to the marked similarity of the diverse types of swarmers, not only in morphological features, but also in respect of size and the type of variability, with those of *Ulothrix*. There can be no doubt that this affords strong presumptive evidence for a common origin of Ulotrichaceae and Chaetophoraceae.

The formation of swarmers generally occurs in the main in the erect system when that is well developed and takes place simultaneously in a large number of cells (fig. 76 A); in *Draparnaldia* whole lateral branches are not uncommonly used up in the process. Usually each cell produces only one to four swarmers and they are mostly liberated through a lateral aperture in the wall (fig. 76 B). Special sporangia are known only in *Pilinia* (128), where they occur as swollen terminal or lateral cells (fig. 76 K, *sp*). Aplanospores (or hypnospores in the case of the microzoospores, fig. 76 D) are frequently observed (55, 118). Palmelloid stages are also known, especially in species of *Stigeoclonium* (29),[1] whilst akinetes are frequent. There is thus the same diversity of reproductive methods as in the Ulotrichaceae. In germination the macrozoospores probably normally first form the basal system (fig. 76 N) from which the upright branches later arise, but in *Draparnaldia* and some species of *Stigeoclonium* it appears that upright threads are formed direct (6, 40, 74, 108, 124 *a*).

Prior to fusion the gametes frequently shed their flagella and become amoeboid (114), and this appears to be the rule in *Draparnaldia* (79) (fig. 76 I). The fate of the zygotes is not known in most cases, but it would seem that commonly at least they germinate directly into new plants (28).

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[1] Livingston (89, 90) showed that *Stigeoclonium* assumes a palmelloid form in solutions of high osmotic pressure and at low temperatures. Vischer ((152 *a*) p. 18) is of the opinion that Livingston's form is a *Pleurastrum* (p. 270).

PROSTRATE TYPES (PROSTRATAE)

The numerous remaining genera of Chaetophoraceae are modified in various ways, the bulk of them being epiphytes on freshwater or marine aquatics (cf. especially (67)). The tendency for reduction of the projecting system evident in some species of *Stigeoclonium* reaches its height in those Chaetophoraceous epiphytes, which, apart from the prostrate system, possess either only a few projecting branches (*Chaetonema*, fig. 80 A) or nothing but hairs (e.g. *Aphanochaete*, fig. 77 A; *Bolbocoleon*, fig. 77 J; *Chaetopeltis*, fig. 79 A; *Gonatoblaste*, fig. 77 G) or have the projecting system completely suppressed (*Endoderma*, fig. 77 D, E; *Pringsheimia*, fig. 78 A; *Protoderma*, fig. 78 I; *Ulvella*, fig. 78 G). It is impossible to describe all the forms involved in detail and a few typical examples must suffice. The cells in all cases possess a single parietal chloroplast which is sometimes reticulate and which contains one or more pyrenoids, except in some species of *Ulvella* and in *Trichophilus*.

Chaetonema irregulare Nowak. ((67) p. 302, (103)), a rare form epiphytic in the mucilage-envelopes of diverse freshwater Algae (*Tetraspora*, *Batrachospermum*, etc.), consists of little branched creeping threads giving rise to short upright filaments which are sometimes branched and each of whose cells bears one or more long unicellular hairs with a slightly swollen base (fig. 80 A). In the common freshwater epiphyte *Aphanochaete*[1] we have prostrate, more or less extensively branched filaments, some or all of the cells of which bear on their dorsal surface one or more erect unicellular hairs (fig. 77 A). In cultures these hairs are sometimes replaced by branches ((25) p. 324), but in nature the upright system is represented only by the hairs which at an early stage lose their protoplasmic contents. *Gonatoblaste* ((67) p. 311), occupying the mucilage of *Zygnema*-threads, is very similar, except that the hairs are stated to be mere outgrowths of the membrane (fig. 77 G, I); they originate at the apices of the terminal cells (cf. fig. 77 I), but gradually come to occupy a dorsal position. *Bolbocoleon* ((67) p. 308, (119)), a marine epiphyte or endophyte, is distinguished by the fact that the hairs arise from special smaller cells, poor in chlorophyll, which occur singly or in groups between the irregularly rounded cells of the creeping threads (fig. 77 J).

A complete reduction of the projecting system is usually found in the endophyte *Endoderma* (= *Entocladia*),[2] the majority of the species of which are marine. The well-branched threads (fig. 77 D, E) grow within the membranes of diverse Algae (*E. Wittrockii* Wille in many

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[1] See (6), (18), (39), (67) p. 278, (78).

[2] See (14) p. 291, (21*a*), (31), (34), (40), (63), (67) p. 313, (125), (168). Schiffner's *Entodictyon* (130) appears to belong to this genus.

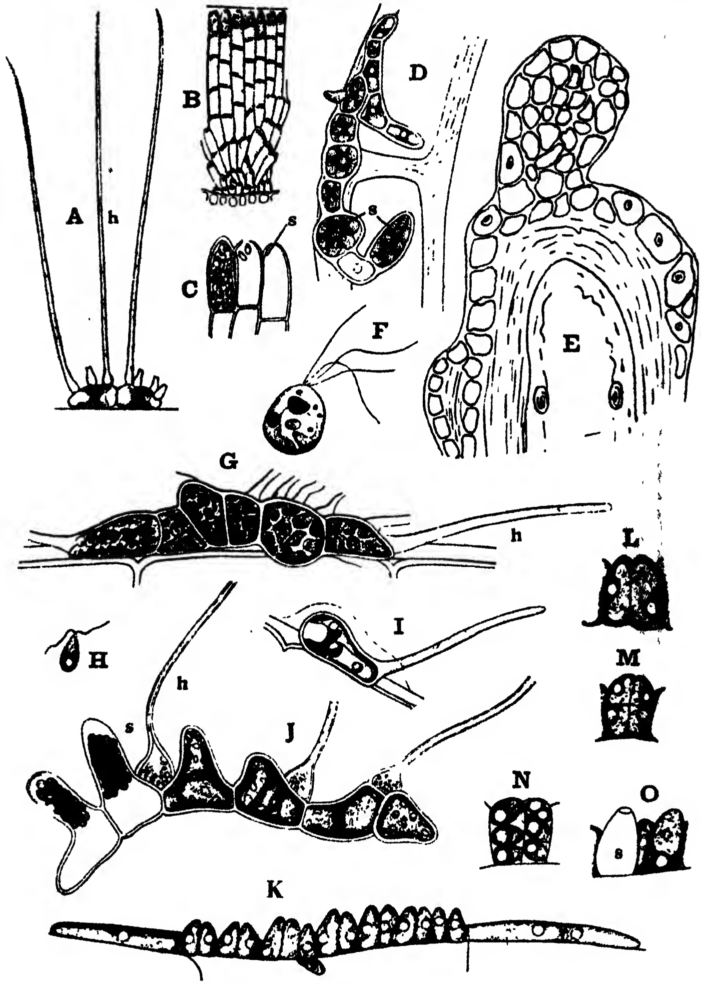

Fig. 77. Types of prostrate Chaetophoraceae. A, *Aphanochaete polychaete* (Hansg.) Fritsch (after West). B, C, *Pseudopringsheimia confluens* (Rosenv.) Wille (after Rosenvinge); B, section of sterile crust; C, sporangia. D, *Endoderma Wittrockii* (Wille) Lagerh. (after Wille), thread with sporangia in membrane of *Ectocarpus*. E, *E. Cladophorae* Hornby (after Hornby), within the membrane of *Cladophora*. F, G, I, *Gonatoblaste rostrata* Hub. (after Huber); F, swarmer; I, germling. H, K–O, *Didymosporangium repens* Lamb. (after Lambert); H, swarmer; K, habit, young sporangia; L–N, stages in development of sporangia; O, dehisced sporangium. J, *Bolbocoleon piliferum* Pringsh. (after Pringsheim), with sporangia. *h*, hair; *s*, sporangium.

Phaeophyceae), while *E. flustrae* Reinke (126) is found in Bryozoa. Especially among the marine forms, the threads often coalesce to form a compact, pseudoparenchymatous, usually one-layered stratum (cf. fig. 77 E). Lambert's *Didymosporangium* (86) is a similar marine epiphyte in which the threads are short and with few or no branches (fig. 77 K). *Trichophilus Welckeri* (154), living within the hairs of the sloth *Bradypus*, is scarcely to be distinguished vegetatively from an *Endoderma*.

The coalescence of the threads of the creeping system seen in certain species of *Endoderma* is characteristic of many epiphytic Chaetophoraceae which thus form more or less rounded discs, often of some size, attached to the substratum; the threads composing the discs are often free from one another at the margins, and the radial arrangement of the cells usually clearly indicates the filamentous origin of the whole. The marine *Pseudopringsheimia*[1] ((172) p. 88), devoid of hairs, forms small cushions in which the short upright threads are densely apposed (fig. 77 B), while the basal cells commonly put out rhizoids which penetrate into the substratum. Wille's *Pseudulvella* ((172) p. 90; *Ulvella* of Snow (142)) forms similar small discs (fig. 78 D) which commonly bear upright threads in the middle (cf. especially *P. consociata* Setchell and Gardner (138)). These types are paralleled by similar ones among the Ectocarpales (e.g. *Ralfsia*) and the Rhodophyceae (e.g. *Hildenbrandia*). In the case of *Trichodiscus* (156) the upright system is represented by numerous short, rarely branched threads and occasional long septate hairs (fig. 78 E), while in the marine epiphyte *Ochlochaete* ((67) p. 290) there are only unicellular hairs which are not cut off by a septum from the parent-cell. The small discs of this genus are composed of two or three layers of rounded cells in the centre which may possibly represent closely adpressed upright threads.

In several epiphytes of this discoid type only the basal system is developed. Thus, *Chaetopeltis*,[2] a freshwater epiphyte which is probably best included here, forms flat, almost circular discs composed of a single layer (rarely two) of radiating or irregularly arranged cells, the whole enveloped in mucilage (fig. 79 A); from the upper surface of the disc there arise a number of irregularly distributed mucilage-bristles (fig. 79 E) which may grow to a great length, but are sometimes altogether absent. In *Pringsheimia* (121 *a*, 126) the central reproductive cells of the mature one-layered discs are more or less wedge-shaped and elongated perpendicular to the substratum, while the marginal cells are flattened and radially elongated (fig. 78 A, C). Long colourless hairs may or may not be present.

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[1] First described as species of *Ulvella* (104, 128).

[2] See (6), (14) p. 329, (21), (67) p. 297, (97). This includes the genus *Myxochaete* of Bohlin (9).

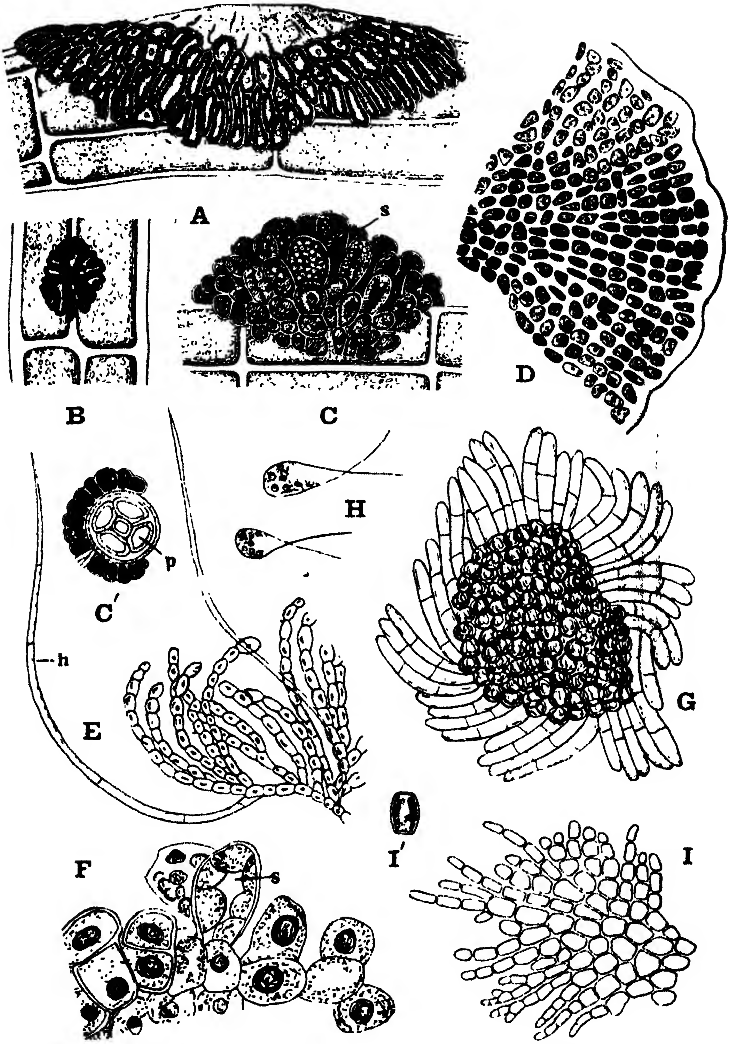

Fig. 78. Types of discoid Chaetophoraceae. A–C, *Pringsheimia scutata* Reinke (after Reinke); A, mature disc with dehisced zoosporangia in the centre; B, young plant on *Polysiphonia*; C′, the same in section; C, thallus with central zoosporangia. D, *Pseudulvella americana* (Snow) Wille (after Snow). E, F, *Trichodiscus elegans* Welsf. (after Welsford); E, part of periphery of disc; F, group of sporangia from centre of disc. G, H, *Ulvella Beesleyi* Fritsch (after Beesley); G, mature thallus; H, swarmers. I, *Protoderma viride* Kütz. (after West); I′, single cell. *h*, hair; *p*, host; *s*, sporangium.

The discs of the freshwater *Protoderma* ((14) p. 245) consist merely of a small central group of polygonal, irregularly arranged cells with short branched filaments radiating from them (fig. 78 I). The independence of *Protoderma* is still in doubt, although its reproduction by zoospores speaks for its being a separate form. In *Ulvella* ((5), (32), (67) p. 294) we have a very similar epiphyte, distinguished by the frequent forked character of the marginal cells, the presence of a more or less copious mucilage-envelope, and especially by the fact that older plants become several-layered in the centre, which is perhaps to be regarded as an almost suppressed formation of upright threads (fig. 78 G). One species of this genus is a common member of the encrusting community in streams (21), while *U. involvens* (Savi) Schmidle (115) is found on the carapace of tortoises. Diverse marine species are known (e.g. *U. lens* Crouan and *U. fucicola* Rosenv. on old plants of *Fucus*).

The numerous prostrate Chaetophoraceae evidently grade into one another and, although they are distinguished by certain differences in reproductive details (cf. p. 264), it may be doubted whether all of them merit a distinct generic status. Too little is, however, as yet known about the majority of them to admit of any definite decision on this point.

THE SPECIALISED ERECT TYPES (ERECTAE)

A few Chaetophoraceae are characterised by the complete absence of a prostrate system. These mostly give the impression of much reduced, specialised forms, and it may be doubted whether they have any close affinity with one another. In *Microthamnion* (53, 135) the plants consist of well-branched filaments, devoid of hairs, at first attached, later often free-floating. The branches commonly arise unilaterally and are borne at the upper end of the parent-cell, the septum being often formed some distance up the branch (fig. 79 F). The elongate cells have thin cellulose walls and each contains a long plate-shaped parietal chloroplast of a pale green colour and devoid of a pyrenoid (fig. 79 G). Food-reserves are stored in the form of oil. *Microthamnion* has been suspected of belonging to the Xanthophyceae (123), but the equal flagella of the zoospores and the cellulose nature of the membranes are altogether against this view.

The minute freshwater epiphyte *Thamniochaete* ((22), (49), (140) p. 403) consists of short erect filaments, branched or unbranched, the basal cell serving for attachment. The terminal cell and sometimes the subterminal ones bear long unicellular hairs (fig. 79 H, I).[1] In *Raphidonema* ((26), (80), (84), (152 a) p. 79), referred by Printz (122) to the

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[1] It is doubtful whether *T. aculeata* West (166) belongs to this genus.

Ulotrichaceae (cf. also (152 *a*)), we have short, often curved, unattached threads tapering at each end and multiplying by splitting into two (fig. 79 C, D). The elongate cells contain a parietal chloroplast devoid of a pyrenoid. The usual habitat of this alga is on the surface of snow (42, 84), but it has also been found in freshwaters.

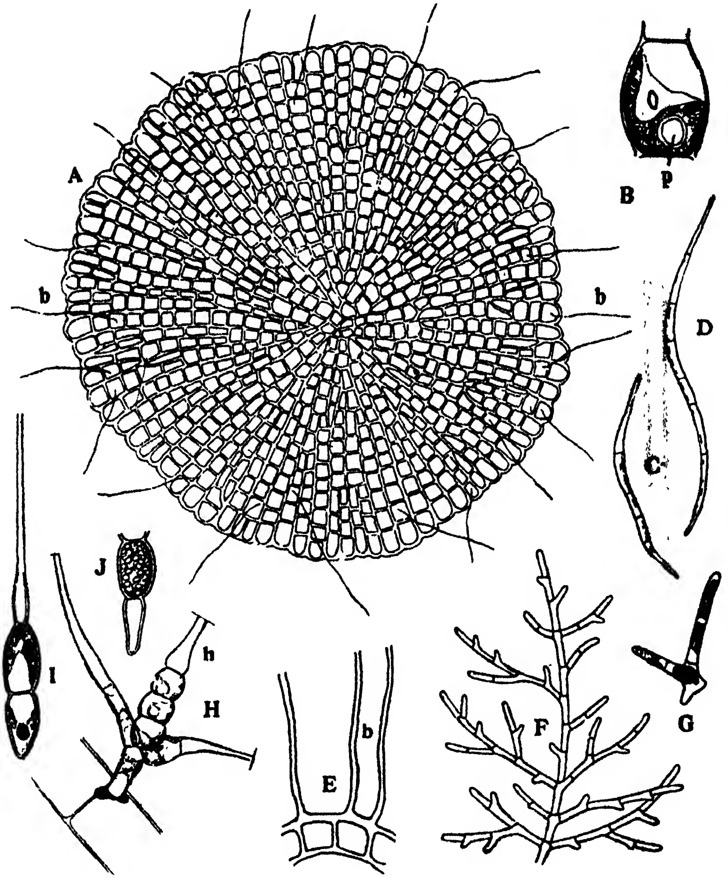

Fig. 79. A, E, *Chaetopeltis orbicularis* Berth.; E, in optical section. B, H–J, *Thamniochaete Huberi* Gay; B, single cell; H, I, two plants, only parts of the hairs are shown; J, akinete. C, D, *Raphidonema nivale* Lagerh. F, G, *Microthamnion Kützingianum* Naeg.; G, a young plant. *b*, mucilage-bristle; *h*, hair; *p*, pyrenoid. (A, E after Berthold; B, H after Chadefaud; C, D after Lagerheim; F, G after West; I, J after Gay.)

REPRODUCTION OF THE SPECIALISED CHAETOPHORACEAE

The majority of the reduced forms considered in the preceding pages are known to propagate by zoospores, usually quadriflagellate (fig. 77 F), but biflagellate in *Didymosporangium* (fig. 77 H), *Ulvella* (fig. 78 H), *Protoderma*, and *Microthamnion*. In most the zoospores are formed in unmodified vegetative cells, but in a few cases the cells producing them become enlarged and appear as more or less clearly differentiated sporangia. This is seen in *Endoderma* (fig. 77 D), *Pringsheimia* (fig. 78 C), *Trichophilus*, and *Ochlochaete*, while in *Didymosporangium* the cells prior to sporangium-formation divide into four, so that the sporangia form characteristic four-celled groups (fig. 77 K–O). In the discoid types (e.g. *Pringsheimia*, fig. 78 A) the zoospores usually arise from the central older cells and in *Ulvella* they are formed in the rounded cells in the middle of the disc (cf. fig. 78 G). In *Pseudopringsheimia* (fig. 77 C) and *Pseudulvella* they are produced mainly in the terminal cells of the upright threads. The number of zoospores produced depends on the size of the cell. They are usually liberated through a well-defined aperture and are sometimes (e.g. *Aphanochaete*) enveloped in a delicate offstanding mucilage-bladder at the moment of being set free. In one species of *Aphanochaete* Pascher (113) records the formation of amoeboid swarmers (fig. 80 H, I). *Thamniochaete* probably likewise reproduces by swarmers (22); structures resembling akinetes (fig. 79 J) have also been recorded in this genus. Aplanospores have only been noted in a few cases. In *Chaetonema* Huber (68) has described palmelloid stages.

Apart from *Chaetonema* and *Aphanochaete*, the gametes where known are isogamous and, except in *Pringsheimia*, appear always to be biflagellate. In some cases (e.g. *Bolbocoleon*) their sexual nature is in doubt, and in the same way it is possible that the biflagellate swarmers of *Didymosporangium* are actually gametes. In *Trichodiscus* (fig. 78 F) the gametes are produced in special gametangia formed on the upright threads. The sexual individuals of *Pringsheimia* (126) are distinguished from the asexual ones by thin walls and the ultimate development of spaces between the cells. Whether this possibly implies a definite alternation remains to be seen.

In *Aphanochaete* (69) there is marked sexual differentiation. Oogonia are developed from enlarged globular cells devoid of hairs in the centre of the creeping filaments (fig. 80 J, *o*) and each gives rise to a single spherical, deep green, quadriflagellate macrogamete containing a large and prominent oil-globule (fig. 80 G); this is expelled by the rupture of the wall. The antheridia are produced at the ends of the filaments and are small and commonly almost colourless (fig. 80 J, *a*). Each gives rise to one or two spermatozoids (fig. 80 F) which are pear-shaped, provided with four flagella and a minute

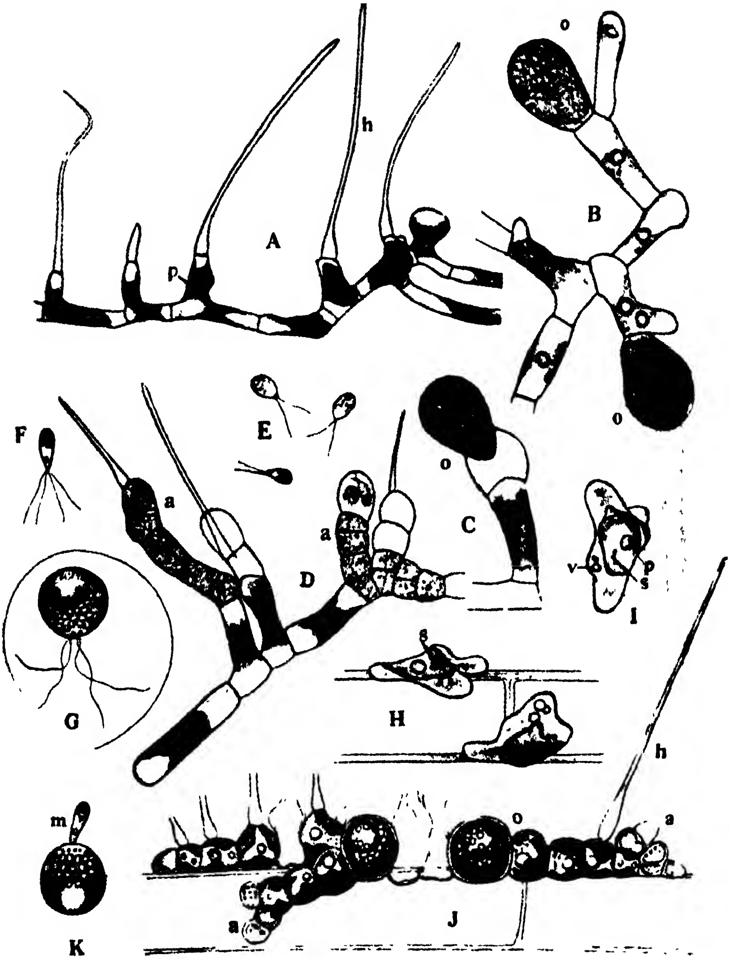

Fig. 80. Oogamous Chaetophoraceae. A–E, *Chaetonema irregulare* Nowak. (after Meyer); A, habit; B, plant with oogonia; C, liberation of ovum; D, plant with antheridia; E, spermatozoids. F, G, J, K, *Aphanochaete repens* A. Br. (after Huber); F, microgamete; G, macrogamete; J, plant with oogonia and antheridia; K, fertilisation. H, I, *A. Pascheri* Heering (after Pascher), amoeboid swarmers. *a*, antheridia; *h*, hair; *m*, microgamete; *o*, oogonium (or ovum); *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole.

chloroplast, and are liberated into a hyaline vesicle which soon becomes diffluent. The spermatozoids exhibit active movement, but the female gametes are sluggish and come to rest prior to fertilisation (fig. 80 K). The oospores are thick-walled with red contents; their germination has not yet been observed. Many authorities (106, 122) place *Aphanochaete* in a separate family, but its anisogamy is so plainly derivable from the isogamy of other Chaetophoraceae that this appears unwarranted.

This point of view is confirmed by the recent discovery of a similar heterogamous sexual reproduction in *Chaetonema* (95). This form develops oogonia and antheridia on distinct plants. The oogonia, formed on lateral branches, are swollen cells (fig. 80 B, *o*) whose contents become filled with food-reserves and constitute a single ovum devoid of flagella. This is set free through a terminal opening (fig. 80 C). The antheridia (fig. 80 D, *a*) are formed by transverse and longitudinal division of the vegetative cells into eight parts (cf. the plurilocular sporangia of Brown Algae), each of which liberates a yellowish green biflagellate spermatozoid (fig. 80 E). Fusion has not been observed. *Chaetonema* in the absence of flagella on the ova shows an advance on *Aphanochaete*, but the fact that the ovum is liberated prior to fertilisation stamps the oogamy as relatively primitive.

It is of interest that among the Chaetophoraceae heterogamy should alone be found in two prostrate types, and this altogether supports the view that these prostrate forms are specialised, while those with a marked upright system are the more primitive.

(*b*) THE FAMILY TRENTEPOHLIACEAE

The series of forms included in this family, in which hairs are only rarely developed, appear to have undergone less reduction, since the majority of the genera possess a thallus with both prostrate and projecting systems, often combining to form dense cushion-like growths. The swarmers in nearly all cases are produced in sporangia or gametangia which are more or less sharply differentiated from the vegetative cells. The Trentepohliaceae also show specialisation in other directions, to wit the frequent incrustation with carbonate of lime in *Gongrosira* and related genera, the capacity for penetrating into calcareous and other substrata in *Gomontia* and *Tellamia*, and the wind-dispersal of the sporangia in the terrestrial *Trentepohlia*.

THE GONGROSIREAE

Among these essentially aquatic forms, the genus *Gongrosira* (129, 136, 169) may be regarded as constituting a central type. Its species are found in fresh, brackish, and salt water, while one (*G. terricola*

Bristol (19)) has been recorded from cultivated soils. The most usual habitat is at the margin of ponds, lakes, and on the stones in rivers where the plants form a tough green stratum; sometimes they are found on the shells of aquatic Gastropods. The plants appear as small cushions or as more spreading growths, which are frequently encrusted with lime and may sometimes form quite a hard stratum (*G. Scourfieldii* West (163)). Weber van Bosse (155) has described the living together of what is probably a species of this genus (*G. spongophila* = *Trentepohlia spongophila* Web. v. Bosse) with the sponge *Ephydatia*.

Attachment to the substratum is effected by a more or less pseudoparenchymatous, one- or several-layered base formed by the confluence of the prostrate filaments and giving rise to numerous short, densely clustered, upright, branched threads (fig. 81 A). The cells, which are often of irregular shape, possess thin or thick stratified walls and contain a single, usually ill-defined parietal chloroplast with one or more pyrenoids (fig. 81 H).

The sporangia are usually terminal on the upright threads (fig. 81 F, G), although intercalary ones also occur. In one group of species (*Ctenocladus* of Borzi (13) p. 27) they are scarcely differentiated from the ordinary cells and form few swarmers (fig. 81 C), whilst in the remainder (*Eugongrosira*) they are much enlarged cells which give rise to numerous zoospores. The latter are biflagellate, ovoid, and slightly flattened (fig. 81 E). Swarmers, believed to be gametes and likewise biflagellate, are produced in the lower cells of the upright threads. Akinetes are not uncommon and are generally formed from the cells of the prostrate system (cf. fig. 81 D).

The cushion-like growths of *Chlorotylium* ((56), (125), (140) p. 398),[1] which are likewise often encrusted with carbonate of lime, are found attached to rocks, etc., in fast-flowing streams. The chief distinctive feature is a characteristic concentric zoning of the upright system (fig. 81 B), due to the alternation of short cells with dense green contents and of elongate cells poor in chlorophyll, this differentiation taking place at about the same level in all the densely apposed threads. Biflagellate swarmers are formed from slightly enlarged terminal cells, while others with four flagella are produced from akinetes which are set free by gelatinisation of the threads.

Similar, but not encrusted cushions are found in *Leptosira* ((13) p. 17), where the threads are markedly torulose and the cells contain a pale yellow-green chloroplast without a pyrenoid (fig. 82 C). Biflagellate swarmers are here formed by simultaneous division of the protoplast

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[1] Howe (64) describes what he believes to be a fossil ally of this genus from the Lower Eocene under the name of *Chlorotylites*. In the absence of the necessary evidence as to cell-contents such an affinity must be highly problematical.

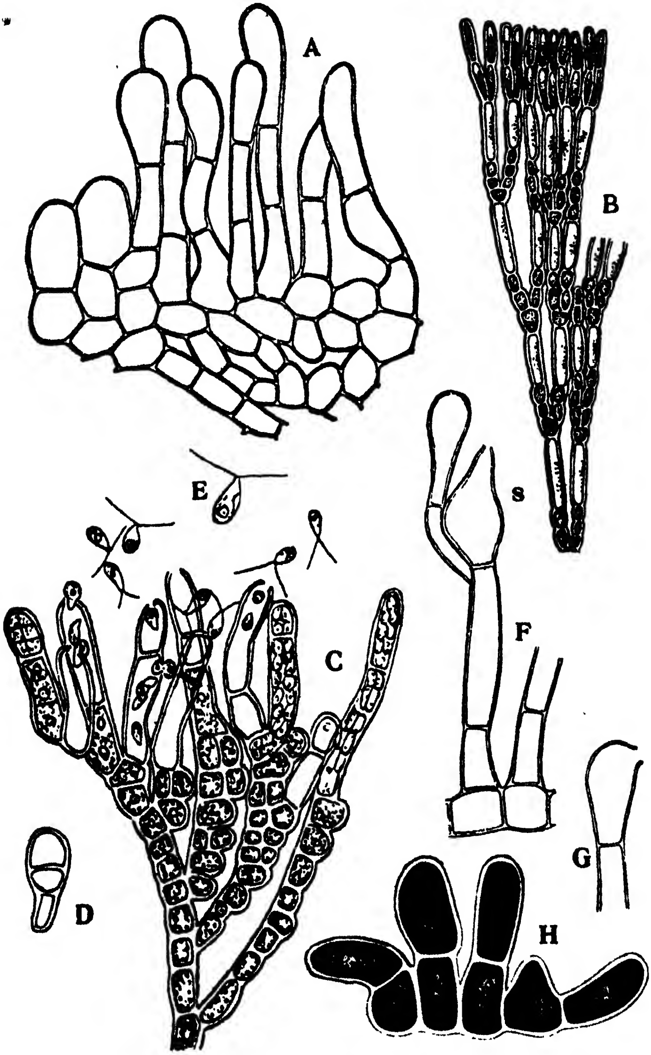

Fig. 81. A, F, G, *Gongrosira stagnalis* (West) Schmidle (after West); F, G, with dehisced zoosporangia. B, *Chlorotylium cataractum* Kütz. (after Migula). C, E, *Gongrosira circinnata* (Borzi) Schmidle (after Borzi); C, formation of zoospores; E, zoospore. D, H, *G. Debaryana* Rabenh. (after Wille); D, germinating akinete; H, young plant. *s*, sporangium.

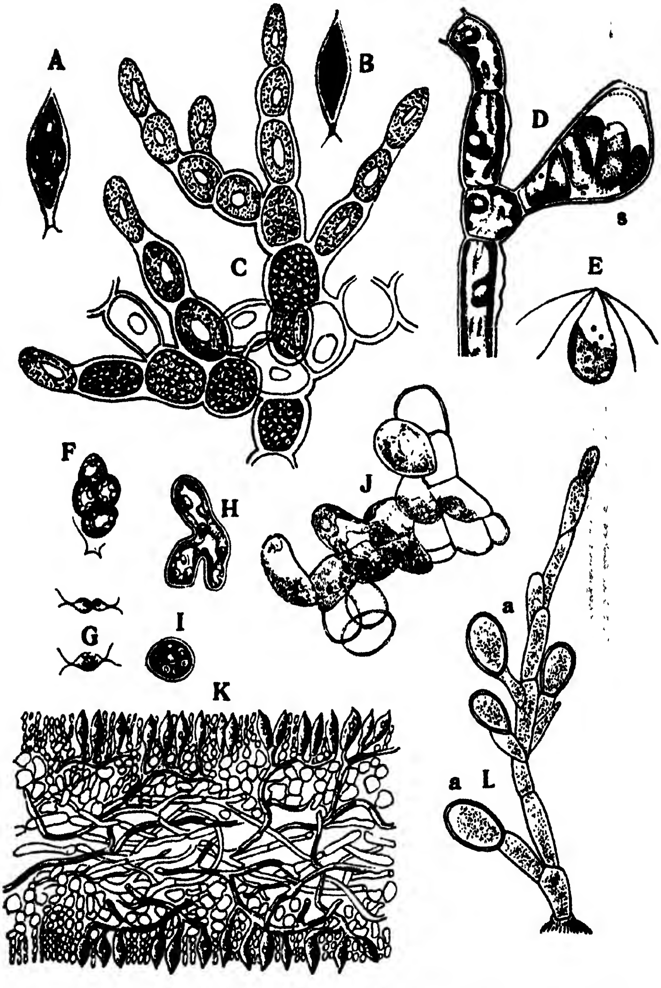

Fig. 82. A–C, F–I, *Leptosira Mediciana* Borzi (after Borzi); A, formation and F, liberation of aplanospores from germling of zoospore; B, such a germling; C, part of a plant forming swarmers, the contents have already escaped from some of the cells; G, sexual fusion; H, germinating aplanospore; I, zygote. D, E, *Sporocladus fragilis* Kuck. (after Kuckuck); D, thread with mature sporangium (*s*); E, swarmer. J, *Pleurastrum insigne* Chod. (after Chodat). K, *Endophyton ramosum* Gardn. (after Gardner), section of *Iridaea laminarioides* with the endophyte. L, *Lochmium piluliferum* Printz (after Printz), with akinetes (*a*).

of any cell and are liberated through a lateral aperture. These zoospores are stated to give rise to *Characium*-like stages (fig. 82 B) whose contents divide to form a number of aplanospores (fig. 82 A, F) which produce new plants. Gametes indistinguishable from the zoospores fuse to form a zygote whose further fate is unknown (fig. 82 G, I). The reproduction of the two genera just mentioned is in great need of reinvestigation. Vischer ((152 *a*) p. 83) describes a second species of *Leptosira* in which only zoospores that germinated directly were observed.

In a number of forms that appear to belong here there is no prostrate system. Such are: Borzi's *Chloroclonium* ((14) p. 303), epiphytic in the mucilage-envelopes of various freshwater Algae and only known from Italy; Kuckuck's *Sporocladus* (81), found on rocks on the coast of Heligoland (fig. 82 D); and Printz's *Lochmium* (120), an epiphyte found in fresh and brackish marshes in Southern Siberia (fig. 82 L). *Sporocladus* (fig. 82 D) has sharply differentiated lateral or terminal sporangia producing a small number of quadriflagellate swarmers (fig. 82 E), while *Lochmium* (fig. 82 L) forms characteristic ovoid akinetes (*a*) terminally on the branches.

The terrestrial *Pleurastrum*[1] ((23), (152 *a*) p. 16), on the other hand, possesses only the basal system and propagates by biflagellate zoospores;[2] it is clearly a markedly reduced form whose exact affinities are difficult to establish (fig. 82 J). Two interesting endophytes in marine Algae are *Pseudodictyon* and *Endophyton* (47), the former inhabiting *Laminaria*, the latter diverse Florideae. In either case the more superficial threads bear short upright branches which extend up to the surface of the host and form terminal sporangia (fig. 82 K).

THE GOMONTIEAE

In the genus *Gomontia* the normal polarity of the thallus of Chaetophorales appears to be inverted, since the often almost pseudoparenchymatous prostrate system composed of very irregular cells (fig. 83 D) grows immediately within the surface-layers of the substratum, while it gives rise on its lower side to threads with very elongate cells which penetrate deeply into the latter (fig. 83 A, B). The structure might also be interpreted as one in which the upright system is suppressed, while the rhizoids found on the underside of some Chaetophoraceous epiphytes have become specially developed to form the penetrating threads. The cells contain a single parietal chloroplast and are commonly multinucleate.

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[1] The genus *Pseudopleurococcus* of Snow (143) is often included in *Pleurastrum* (cf. however (152 *a*) p. 17).

[2] A very similar form is *Pseudendoclonium* ((152 *a*) p. 21, (170 *a*)) in which, however, the swarmers are quadriflagellate.

The substratum may be calcareous, woody (100), or composed of dead algal cells. *G. perforans* (Chod.) Acton (*Foreliella perforans* Chodat (24) p. 434) inhabits the shells of living Mollusca in various Swiss lakes, while *G. codiolifera* (Chod.) Wille[1] (*Gongrosira codiolifera* Chodat (24) p. 443) has been found on calcareous rocks in the Lake of Geneva. Acton (1) has described another freshwater species (*G. Aegagropilae*) found in dead *Cladophora holsatica* "balls" from Scotland. *G. polyrhiza* (Lagerh.) Born. et Flah. is widely distributed in the northern hemisphere in the empty shells of marine Molluscs (12, 171).

In all cases the alga is recognisable as green specks which cannot be rubbed off. In the species inhabiting shells the penetrating threads often extend right through their substance, and in *G. polyrhiza* form a secondary prostrate system on the inner surface, while Chodat describes them as terminating in characteristic enlargements in *G. perforans* (fig. 83 E). The penetration of the threads is of course due to solution of the lime by the growing tips and, when large numbers of the threads grow near together, the substance of the shells gradually crumbles until complete disintegration occurs.

The reproductive elements are in part formed in much enlarged cells, which appear usually to be lateral outgrowths of the prostrate system (fig. 83 F) and extend into the interior of the substratum (fig. 83 C). Ultimately they generally develop a certain degree of independence, forming special basal attaching rhizoids of their own which have thick lamellate walls (fig. 83 I); the whole sporangium then often strikingly resembles a *Codiolum* and has indeed been described as such (83). Sporangia, producing 2–4 ovoid quadriflagellate zoospores and not appreciably enlarged, have been noted in certain species, while the large structures just described either form numerous aplanospores or large numbers of pear-shaped biflagellate swarmers of different sizes which are suspected of being gametes, although their fusion has not yet been established. The aplanospores either grow direct into new plants or, after liberation or sometimes even within the sporangium itself (fig. 83 J), give rise to other aplanosporangia. Acton records akinetes (fig. 83 H, *a*), while Nadson (101) describes palmelloid stages in *G. polyrhiza*.[2]

The genus *Tellamia* ((4), (121 *a*) p. 236) which lives in the periostracum of the shells of marine snails, but does not penetrate into the calcareous portion, has a creeping system of deep olive-green branched threads. From these arise vertical branches which are short and pointed (fig. 83 L) and grow either towards the inside or the

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[1] Zimmermann ((174) p. 20) expresses doubts whether this alga is lime-boring and believes it to be a *Gongrosira*.

[2] Pratje (116) believes he has recognised fossil forms in the Lias, but as he himself points out they might just as well belong to Blue-Green Algae.

probably of frequent occurrence. In *T. umbrina* the rounded or ellipsoidal cells of the prostrate system readily separate from one another (fig. 85 B), forming a fine dust which is no doubt dispersed by the wind. Irgang (70) mentions that in *T. Iolithus* the majority of *the cells of the threads die off during dry periods, leaving only occasional cells rich in haematochrome which presumably serve for* purposes of propagation. Abundant reproduction during wet weather no doubt also occurs by means of swarmers, although there is some evidence that such propagation only takes place at certain times of the year (65). The swarmers are formed in special ellipsoid or ovoid sporangia which are of two or possibly three kinds (15, 16, 76, 93 *a*).

The simplest are the *sessile sporangia* (fig. 84 A) which occupy very diverse positions; they may be terminal, lateral, intercalary, or rarely axillary (*a*). They are formed merely by enlargement of a cell and, unlike the other types, liberate their swarmers without detachment. The *stalked sporangia* (fig. 85 H, I) appear only as terminal or lateral appendages and are formed by the cutting off of a tubular outgrowth (fig. 85 J, K) from a somewhat enlarged supporting cell which may give rise to several such sporangia (fig. 85 I). The apical part of the outgrowth swells up to form the sporangium which then becomes separated from the stalk-cell below, which is often bent in a characteristic knee-shaped manner. The intervening septum develops two concentric ring-shaped cellulose thickenings (fig. 85 N), the one peripheral (*o*), the other more central (*i*). The stalked sporangia appear usually to become detached (fig. 85 M) and to be wind-dispersed, the liberation of the swarmers taking place on subsequent wetting. Quite similar sporangia occur in *Cephaleuros* (p. 280).

The mode of detachment is not altogether clear, especially as regards the rôle played by the thickening rings on the septum; it seems that the latter splits, as well as the rings (cf. fig. 85 L). The third type of sporangium ("*funnel-sporangium*" of Brand (16)) is produced terminally from the apex of a cylindrical cell (fig. 85 O), the septum that cuts it off lying between two superposed thickening rings (fig. 85 P, *u*, *l*). The outer layer of the original cell-wall splits at the level of the septum, so that these sporangia likewise become detached at maturity. As Oltmanns ((106) p. 326) suggests, these funnel-sporangia may be but a modification of the stalked sporangia. It is not at present known what kinds of reproductive cells are formed by the funnel-sporangia.

The stalked sporangia produce a considerable number of bi- or quadriflagellate swarmers liberated through a terminal or lateral aperture which is usually somewhat protruded (fig. 85 H, M). The somewhat flattened swarmers appear always to germinate direct (76).

The sessile sporangia invariably produce biflagellate swarmers (fig. 85 E) and in certain cases they have been observed to behave as isogametes ((82), (167); cf. also (76) p. 53) (fig. 85 F), although they can

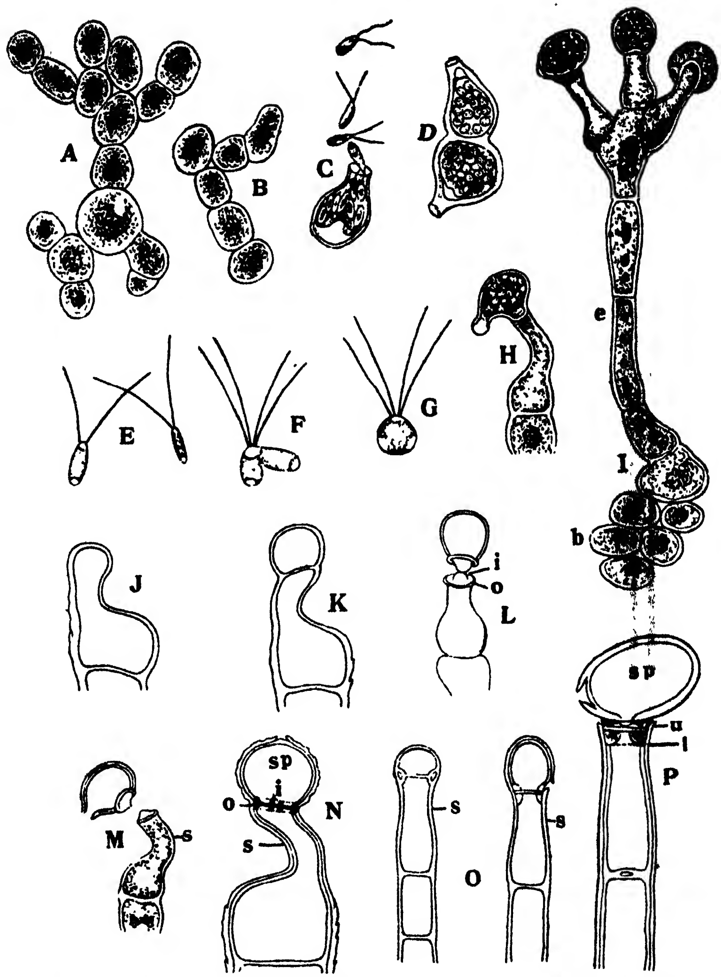

Fig. 85. Reproduction of *Trentepohlia*. A–D, H, I, L, M, *T. umbrina*; E–G, *T. Bleischii* (Rabenh.) Wille; J, K, N, *T. Iolithus*; O, P, *T. annulata* Brand. A, B, fragmentation of prostrate system; C, D, gametangia, in C liberating gametes; E, F, sexual fusion; G, zygote; H, stalked sporangium; I, thread with same; J, K, development of same; L, M, its detachment; N, stalked sporangium (diagrammatic); O, two stages in development of a funnel-sporangium; P, the same mature (diagrammatic). *b*, prostrate and *e*, erect systems; *i*, inner and *o*, outer thickening of sporangial septum; *l*, lower and *u*, upper rings of thickening; *s*, stalk-cell; *sp*, sporangium. (C, D after Karsten; E–G after Wille; J, K, N–P after Brand; the rest after Gobi.)

also germinate without fusion or give rise to aplanospores (93 a). There is therefore some justification for regarding this type of sporangium as a gametangium. Unlike the stalked sporangia, these structures are not uncommonly produced on the basal parts of the plant (cf. fig. 84 A); this is often the case in species of the section *Heterothallus*. Here inundation admitting of sexual fusion will readily occur, whilst the usual production of the stalked sporangia on the erect threads admits of an easy wind-distribution. In many cases stalked and sessile sporangia occur on the same individual, but it seems that not uncommonly they are found on distinct plants which suggests the possibility of an alternation. The two types of individuals may, moreover, seemingly show other differences; thus, while the usual individuals of *T. umbrina* (fig. 85 A) produce only sessile sporangia from cells of the prostrate system, others appear to develop upright threads bearing stalked sporangia (fig. 85 I) ((10) p. 101, (36), (52), (93)).

Trentepohlia monile de Wildeman, widely distributed in the Tropics, has been placed by Printz (121) in a separate genus *Physolinum*, distinguished by the fact that growth and branching are brought about by a process similar to budding and that the sporangia produce only aplanospores. *Stomatochroon* (175) is a reduced form inhabiting the stomatal apertures of the leaves of tropical plants. The plant consists of a lobed anchoring cell located in the respiratory cavity and a cylindrical thallus cell projecting slightly from the pore; on this are borne a few vegetative threads, as well as typical sporangia like those of *Trentepohlia*. In Dangeard's *Rhizothallus* (35), growing on clayey soil near streams, the prostrate system ramifies to some depth in the substratum. In the absence of reproductive organs its systematic position is uncertain.

In other Trentepohlieae the erect system exhibits extreme reduction. *Phycopeltis*[1] is a small discoid epiphyte, one species of which (*P. epiphyton* Millard., fig. 86 A) has not uncommonly been found on leaves and other parts of *Abies*, *Hedera*, *Rubus*, etc., forming greenish or orange-yellow specks due to the compact one-layered strata. In other species the latter are more plainly composed of anastomosing threads (sect. *Hansgirgia*). Short vertical filaments bear the detachable stalked sporangia which give rise to biflagellate swarmers, while smaller biflagellate gametes are formed from the central cells of the prostrate system (fig. 86 A, D, E). *Phycopeltis expansa* is the algal component of the lichen *Strigula complanata*.[2]

The tropical genus *Cephaleuros*[3] comprises both epiphytes and parasites, usually found on the leaves of Phanerogams. The thallus consists of one or several layers of branched interwoven threads with

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[1] See (73), (76), (96), (99), (132).

[2] There is some confusion as to the genera of Algae forming the gonidia of this Lichen (see (91) p. 60; and p. 280).

[3] See (57), (76), (134), (147).

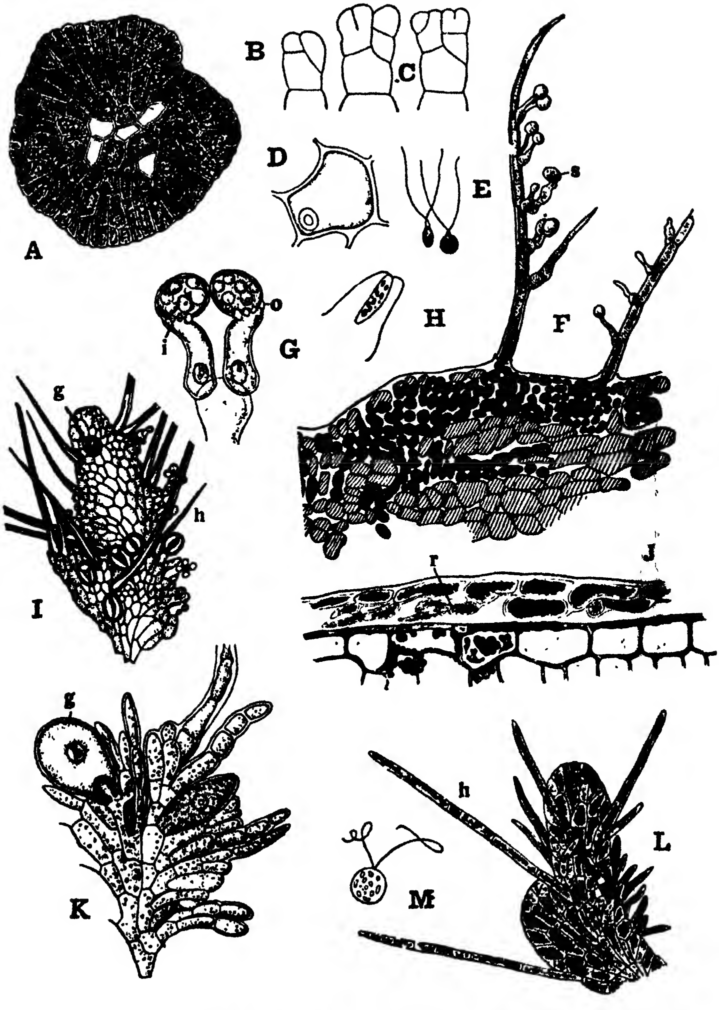

Fig. 86. A–E, *Phycopeltis epiphyton* Millard.; A, a plant from five of whose cells gametes have escaped; B, C, parts of margin of disc; D, gametangium; E, gametes. F, *Cephaleuros minimus* Karst. in leaf-tissue of *Zizyphus*, erect threads bearing stalked sporangia (*s*). G, H, J, L, M, *C. virescens* Kunze; G, stalked sporangia; H, young and M, older gametes; J, epidermis of *Michelia fuscata*, showing the alga and its rhizoids (*r*); L, part of a disc. I, K, *C. laevis* Karst., discs with gametangia (*g*). *h*, hair; *i*, *o*, inner and outer thickenings of septum of stalked sporangium. (A–E after Millardet; H, J, L, M after Marshall Ward; the rest after Karsten.)

apical growth which usually form a more or less compact stratum (fig. 86 J, L). Vertical threads, which project to the exterior in the case of the parasitic forms and are often unbranched, bear lateral clusters of stalked sporangia like those of *Trentepohlia* (fig. 86 F, G). In certain species sterile projecting branches ending in hairs are produced (fig. 86 L, *h*). In the parasitic forms richly branched unicellular rhizoids arise from the lower cells of the stratum (fig. 86 J, *r*) and ramify in all directions in the tissues of the host (cf. fig. 86 F). Both these and the ordinary threads have been observed within the actual cells (76), but it is not clear whether penetration of the latter occurs before they are dead. The cells contain chloroplasts like those of *Trentepohlia*.

C. virescens Kunze (*Mycoidea parasitica* Cunningh. (33, 76)) is parasitic on leaves of *Camellia*, *Rhododendron*, *Thea*, etc. It is the cause of the "red rust of tea" in north-east India and Assam, one of the most serious diseases to which the tea-plant (*Thea sinensis*) is subject; it is most destructive as a stem-parasite (92). It attacks both leaves and young shoots, the latter being infected by swarmers formed from the thalli on the leaves. The parasite can only make headway when the host is growing slowly; when the latter is vigorous, the alga is gradually shed by exfoliation of the outer tissues. The same species also attacks the *Piper*-plantations in eastern India (139), and according to Wolf (173) the *Citrus*-trees in Florida, where the tissues beneath the point of infection are stimulated to form wound-cork. *C. Coffeae* Went (157) is parasitic on *Coffea liberica*, the sporangium-bearing threads in this case projecting from both surfaces of the leaf, those on the lower side emerging through the stomata. *C. virescens* is often associated with the lichen, *Strigula complanata*,[1] which is also parasitic (153).

The sporangia of *Cephaleuros* produce biflagellate zoospores, while gametangia, often formed by enlargement from the ordinary cells of the stratum (fig. 86 I, K), give rise to biflagellate gametes (fig. 86 H, M). In the parasitic species the swarmers are washed into the stomata during rain and soon develop a stratum beneath the epidermis which becomes gradually elevated.

The classification of the forms discussed in the previous pages in one family was first advocated (170), but later abandoned by Wille (172). There are of course obvious differences between the Trentepohlieae and Gongrosireae in cell-structure and in the high degree of adaptation to a terrestrial existence exhibited by the former. Some species of *Gongrosira*, however, show considerable resemblance to species of *Trentepohlia* (133). In some respects the Gongrosireae and Gomontieae approach nearer to the Chaetophoraceae with which Printz (122) indeed classifies them. On the other hand the diverse forms here included as Trentepohliaceae appear on the whole to show a higher differentiation

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[1] Cf. footnote 2 on p. 278.

than is usual among the Chaetophoraceae, the occasional differentiation of sporangia among the latter being much more marked in the former. Moreover, many of the Trentepohliaceae show adaptation to special habitats and in this respect also exhibit a greater specialisation than do the Chaetophoraceae. It is especially *Microthamnion* among the latter, whose correct position is in doubt and which shows perhaps greater resemblances with the Gongrosireae.

(*c*) THE FAMILY COLEOCHAETACEAE

The abundant freshwater epiphyte *Coleochaete*,[1] with about ten species, is the only representative of this family. Like so many other oogamous Green Algae it occupies a rather isolated position. Some species (e.g. *C. pulvinata*, fig. 87 F) possess a typical heterotrichous habit, the numerous filaments of the projecting system combining to form a hemispherical cushion which is usually enveloped in mucilage. In most species, however, only the prostrate system is represented, either appearing as loosely arranged branching threads (*C. divergens*, fig. 87 H; *C. Nitellarum*) or as more or less circular discs in which the creeping threads are arranged radially and are attached (always?) by slender outgrowths of the walls adjacent to the substratum (158). In the latter case the individual threads may be readily distinguishable (*C. soluta* Pringsh.) or they are congenitally fused to form a compact one- (sometimes two- or three-) layered stratum (*C. scutata*, fig. 87 A). *C. Nitellarum* (75, 87) often grows endophytically beneath the cuticle of Characeae. The growth is always apical, taking place by means of a marginal meristem in the discoid types. Branching of the threads is either effected by lateral outgrowth or by dichotomous division of the apical cells.

The cells are uninucleate and possess a large parietal chloroplast of irregular shape with one or two prominent pyrenoids (fig. 87 E); this is normally apposed to the dorsal wall. Usually every cell bears a characteristic sheathed bristle (fig. 87 C–E) which, according to Wesley ((158) p. 16), is initiated by the development of a pore in the outer wall, followed by the secretion of a continuous membrane over the protoplast. Opposite the pore a deeply staining granule (sometimes two) arises from which a dense finely granular mass issues, passing into a protrusion formed by the outgrowth of the new membrane through the pore. Ultimately this protrusion ruptures apically and remains as the sheath about the central cytoplasmic thread which continues to elongate to form the bristle. The base of the sheath enlarges and extends into the cell as a knob-like structure. The bristles readily break off and on older plants one often finds only the basal sheath.

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[1] See (24) p. 457, (75), (105), (117).

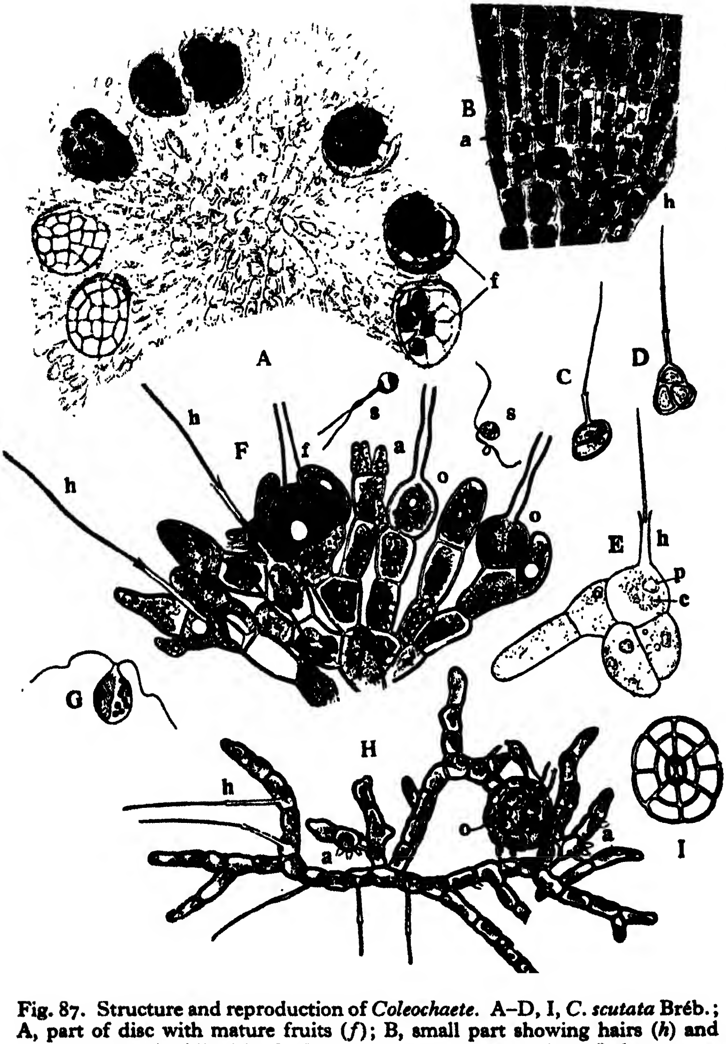

Fig. 87. Structure and reproduction of *Coleochaete*. A–D, I, *C. scutata* Bréb.; A, part of disc with mature fruits (*f*); B, small part showing hairs (*h*) and developing antheridia (*a*); C, D, young stages in side-view; I, later stage from above. E, F, *C. pulvinata* A. Br.; E, young thallus; F, part of erect system with hairs (*h*), oogonia (*o*), and antheridia (*a*); at *f* the envelope is forming around the oogonium; above two spermatozoids (*s*). G, *C. Nitellarum* Jost, zoospore. H, *C. divergens* Pringsh., with antheridia (*a*) and oogonia (*o*). *c*, chloroplast; *p*, pyrenoid. (E after Chodat; G after Jost; the rest after Pringsheim.)

Asexual reproduction (117, 158) is effected in spring and early summer by large ovoid biflagellate zoospores which are formed singly in the ordinary cells and escape through a round opening formed at the apex of a short papilla. The zoospores (fig. 87 G) are peculiar in frequently having the single chloroplast placed laterally; they lack an eye-spot. In germination the swarmer divides either horizontally into two overlying cells of which the upper merely forms a hair, while the lower segments in two directions at right angles to the substratum to form the disc (*C. scutata*, fig. 87 C, D), or vertically into two cells which constitute the centre from which the creeping threads develop. The zoospores of *C. Nitellarum* put out a tubular prolongation which pierces the cuticle of the host and produces the threads which push their way between the layers of the wall.

The sexual reproduction, which in European regions usually takes place from May to July, exhibits the most specialised type of oogamy found among the Green Algae. In *C. pulvinata* (fig. 87 F) the oogonia (*o*) are formed terminally on short lateral branches of the projecting threads, but are usually subsequently displaced to one side by a branch arising from the underlying cell. The oogonium (fig. 88 A) is flask-shaped with a swollen basal portion containing the chloroplast and a long neck (trichogyne) harbouring only colourless cytoplasm. At maturity the tip of the neck breaks down (fig. 88 B), a certain amount of hyaline cytoplasm is exuded, while the basal protoplast rounds off to form the single ovum. In the discoid forms, where the oogonia appear as bulging hemispherical structures with the neck represented at best by a short papilla, they likewise arise terminally by the enlargement of certain marginal cells. The surrounding ones continue the peripheral growth of the disc, so that the oogonia later appear intramarginal (fig. 87 A) and, since two or more series may develop consecutively, they are found arranged in rough concentric zones.

The antheridia of *C. pulvinata* are borne in clusters at the ends of branches of the projecting system (figs. 87 F; 88 C, *a*), often on the same main thread that bears an oogonium. They arise as small colourless outgrowths which become cut off from the parent-cell. Not uncommonly similar antheridia may be produced at the sides of the underlying cells or even by those below an oogonium. In most of the discoid species they occupy a comparable position at the margin of the disc, but in *C. scutata* (159) they originate from some of the products of division of an intercalary cell (fig. 87 B). Each antheridium produces a single colourless spermatozoid (sometimes green in *C. scutata*), which is oval or spherical in shape (cf. fig. 87 F, *s*), and provided with two apical flagella. The male cells are set free by breaking down of the apex of the wall of the antheridium. A few species are dioecious (e.g. *C. scutata*).

After fertilisation the neck of the oogonium becomes cut off by a septum, while the basal part gradually enlarges (fig. 88 H). At the same time the oogonium becomes overgrown by branching threads originating from the underlying and other adjacent cells, and these threads ultimately unite to form a complete pseudoparenchymatous investment (fig. 88 E), the walls of which take on a red or reddish brown colour. In the discoid types (fig. 87 A) this envelope is formed only on the side away from the substratum. A thick brown membrane then develops around the oospore (fig. 88 F) and, according to Oltmanns (105), this is formed partly from the oogonial wall and partly from the inner membranes of the investing threads. Subsequently the cells of the envelope usually die and the oospore hibernates enclosed in its double membrane.

In spring the contents gradually acquire a fresh green appearance and divide into two by a wall perpendicular to the long axis of the original oogonium. Two further walls at right angles afford an octant stage and subsequent divisions result in the formation of 16 or 32 wedge-shaped cells (fig. 88 F). The envelope is then burst (fig. 88 G) and each cell gives rise to a swarmer (fig. 88 D) which, according to Pringsheim ((117) p. 24) and others, differs in no way from the ordinary asexual swarmers.

According to Allen (2) reduction takes place at the first division in the zygote, so that the *Coleochaete*-plant is haploid like so many other Green Algae. Pringsheim ((117) p. 25) reported that the swarmers from the zygotes gave rise to a number of asexual generations before the sexual plant was produced, and the same has been recorded by Lambert (85). This feature is worthy of further enquiry, and a re-examination of the life-history of *Coleochaete*, and especially of other species than that already investigated, is much to be desired.

There are remarkable analogies between the sexual reproduction of *Coleochaete* and that of the Nemalionales among the Red Algae, but these are hardly likely to be due to anything more than homoplasy. In both cases we have a high degree of specialisation and the similarities are no doubt an expression of the general trend which evolution in the lines of algal descent has followed. It is nevertheless significant that such an advanced oogamous differentiation should occur only in the Chaetophorales among Green Algae. The relation to other members of the order is not at all clear, although *Aphanochaete* and *Chaetonema* indicate the manner in which oogamy has evolved within the group.

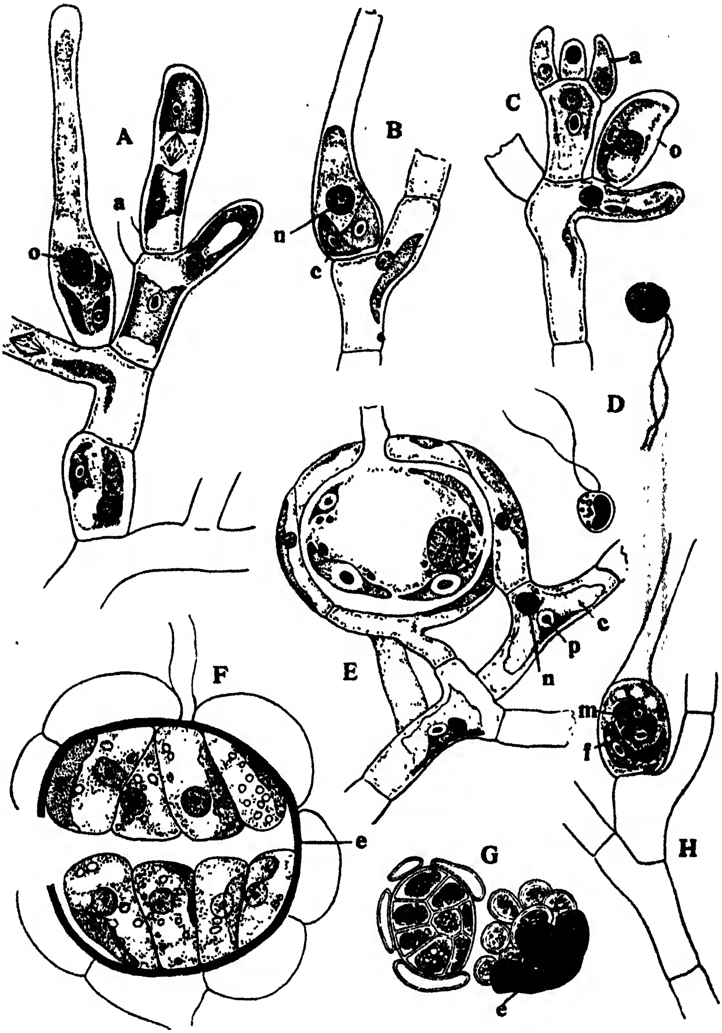

Fig. 88. Sexual reproduction of *Coleochaete pulvinata* (D, G after Pringsheim; the rest after Oltmanns). A, branch with oogonium before dehiscence; B, the same after dehiscence; C, branch with three antheridia and a young oogonium; D, swarmers liberated from zygote; E, formation of envelope around fertilised oogonium; F, germinating zygote; G, two zygotes at a later stage, swarmer-development; H, sexual fusion. *a*, antheridium; *c*, chloroplast; *e*, envelope of zygote; *f*, female and *m*, male nucleus; *n*, nucleus; *o*, oogonium; *p*, pyrenoid.

(*d*) THE FAMILY CHAETOSPHAERIDIACEAE

The Algae comprised in this family are not necessarily closely related to one another, but until their affinities are more clearly established it is convenient to class them together. They are all reduced aquatic forms, mainly living in freshwater, whose only common characteristic lies in the development of one or more solid setae from the membranes of the cells; in some forms (e.g. *Chaetosphaeridium*, fig. 90 A) the setae have a basal sheath, as in *Coleochaete*. Several of the genera consist of loose clusters of unicellular individuals—isolated cells being

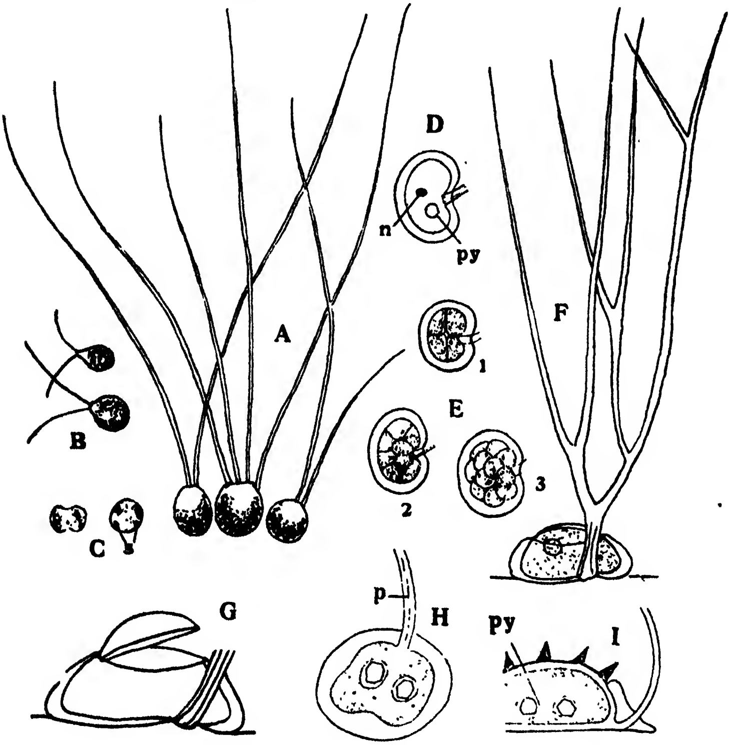

Fig. 89. A, *Oligochaetophora simplex* West (after West). B–I, *Dicranochaete reniformis* Hieron. (B–G after Hodgetts; H, I after Hieronymus); B, two swarmers; C, two zygotes; D, cell-structure; E, *1–3*, three stages in development of swarmers; F, habit; G, dehisced sporangium; H, development of seta; I, the form with a tuberculate wall. *n*, nucleus; *p*, protoplasmic thread in seta; *py*, pyrenoid; *s*, stigma.

not uncommon—and might with equal justification be referred to the Chlorococcales. Some or all may, however, well represent reduced Chaetophorales. There is usually a single parietal chloroplast.

In West's *Oligochaetophora* (160, 161) the subglobose or ovoid cells are loosely aggregated to form very small colonies with but a slight attachment to the substratum, and each cell bears on its dorsal surface 2–4 long flexuose unbranched setae (fig. 89 A).

The cells of the not uncommon epiphyte *Dicranochaete* (61, 62) are often single and only rarely united into short rows. They are specially characterised by the forked gelatinous setae (fig. 89 F) which are sometimes of considerable length. In *D. reniformis* Hieron. the seta arises from the ventral notch of the kidney-shaped cells, but in *D. britannica* West (162) the cells are globose and bear the setae dorsally. The swarmers of *D. reniformis* ultimately become attached by one side, while the anterior hyaline end grows out as a delicate protoplasmic thread (cf. with pseudocilia) which becomes enveloped in a tube of mucilage; thereupon the protoplast secretes a wall in the usual way (fig. 89 H). When the hair, after repeated forking of the thread, is fully grown the mucilage closes in over the apices of the branches, while the protoplasmic thread is retracted, its place being likewise taken by mucilage (61). The chloroplast lies against the outer wall of the cell which, in *D. reniformis*, often bears a number of conical tubercles (fig. 89 I). The cells by successive division (fig. 89 E) form from four to 32 biflagellate zoospores (fig. 89 B) which are liberated by the detachment of a lid (fig. 89 G). According to Hodgetts (62) these swarmers may occasionally behave as gametes giving rise to a quadriflagellate zygote which, like the zoospores, soon comes to rest (fig. 89 C). Resting stages enveloped by a thick membrane are formed from the contracted protoplast.

Among the forms with sheathed bristles the commonest is *Chaetosphaeridium* (77, 78) which occurs as single cells or more commonly as aggregates of spherical cells, sometimes enveloped in mucilage, attached to larger Algae and other aquatics. The cells are united to form short creeping filaments in which the individual cells are often separated by empty cylindrical tubes (fig. 90 A). These arise by horizontal division of a cell, the lower daughter-cell then migrating to one side or developing a tubular outgrowth (fig. 90 B) into which the protoplast passes, the apical part becoming cut off from the empty part behind. Each cell bears on its free surface an often very long and delicate seta surrounded by a basal sheath formed by the ruptured outer layers of the wall; the fragile setae commonly break off. Reproduction is effected by zoospores, four of which are formed in a cell.

Conochaete (78, 135, 166) is a similar form with loosely aggregated cells, each bearing a number of long setae which radiate in all directions and arise from the apices of conical sheaths (fig. 90 C). The cells multiply by division and the formation of zoospores. Suessenguth (145) has recorded the occurrence of a species of this genus within the thallus of *Peltigera*.

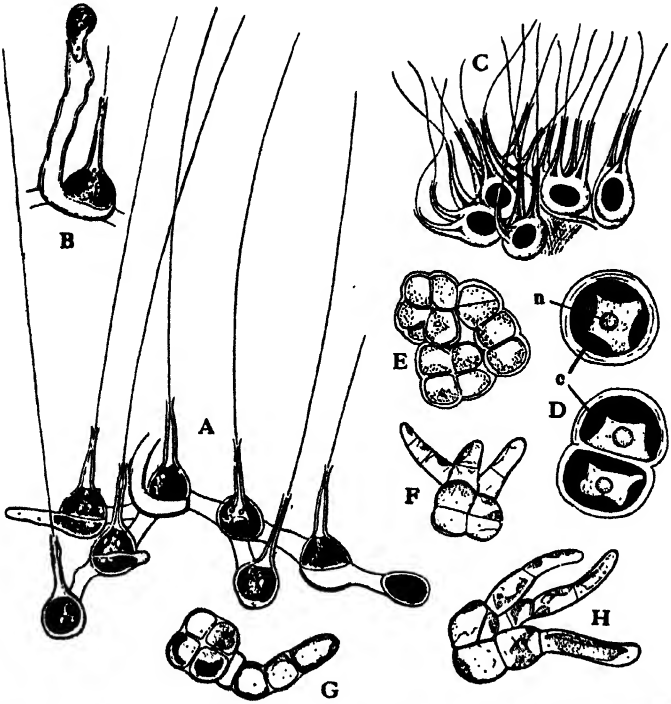

Fig. 90. A, B, *Chaetosphaeridium minus* Hansg.; B, escape of probable swarmer. C, *Conochaete comosa* Kleb. D–H, *Pleurococcus Naegelii* Chod.; D, cell-structure; E, normal packet; F–H, thread-formation. *c*, chloroplast; *n*, nucleus. (A–C after Klebahn; D after Fritsch & Salisbury; the rest after Chodat.)

(*e*) THE GENUS *PLEUROCOCCUS*

Pleurococcus is the commonest, and probably best regarded as the only, genus of the family Pleurococcaceae. It is an ubiquitous terrestrial alga, occurring in great profusion in all kinds of damp situations as a thin incrustation on the windward side of stones, walls, palings, tree-trunks, etc. The cells can withstand prolonged desiccation without change (45), and there is no evidence of the occurrence of special resting stages; this alga probably covers most of its moisture-requirements by the absorption of atmospheric vapour (131).

The common terrestrial form is *P. Naegelii* Chodat (27) (*P. vulgaris* Naeg. non Menegh.; *Chlorococcum vulgare* Grev.; *Protococcus viridis* Ag.).[1] The mature cells are isolated and more or less globose, but they are frequently found in groups of two, three, four or more (fig. 90 D, E) owing to slow separation of the products of division. In moist places short filaments (3, 25, 26) with a few branches (fig. 90 F–H) are often produced as a result of division mainly in one direction, such filaments readily arising in cultures. The cell-wall is firm without usually being appreciably thickened, while the protoplast is without obvious vacuoles (45) and contains a single parietal, more or less lobed, and often massive chloroplast without a pyrenoid (fig. 90 D, E). The sole method of reproduction certainly established is by vegetative division in three directions followed by subsequent separation of the cells.

There is probably no other algal genus about which there has been so much confusion. Many of the species that have been ascribed to *Pleurococcus* belong to *Chlorococcum*, *Chlorosphaera*, *Trebouxia* (*Cystococcus*), or *Chlorella*, or even to other algal classes, and until relatively recent times any globose unicellular form that could not be placed elsewhere was described as a species of *Pleurococcus* (or *Protococcus*), often without any evidence as to its detailed cell-structure or its mode of reproduction. There is little proof that unicellular non-palmelloid forms, endowed with the capacity of limitless vegetative division, occur in other than terrestrial situations, and one may hazard a conjecture that all the aquatic "species" of *Pleurococcus* belong to other genera. Further, it is probable that the records of zoospores and gametes in the true terrestrial species of the genus are due to confusion with *Chlorococcum* and *Trebouxia*, which often grow intermingled with *Pleurococcus*, although there is no *prima facie* reason why the latter should lack them.

It is still debatable whether there is more than one species of *Pleurococcus* of frequent occurrence in terrestrial situations. The common form has a somewhat lobed parietal chloroplast without a pyrenoid; there is, however, possibly another similar alga in which a pyrenoid is

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[1] With reference to the complex synonymy, see *British Freshwater Algae* ((164) pp. 210 et seq.).

present. Possibly the two are but different races of the same species. The writer is, however, of the opinion that the majority of the stages figured by Chodat (25) as *P. vulgaris* Menegh., as well as some shown by West ((162a) p. 192) and others ((20) p. 585), belong to *Trebouxia*. The true *P. vulgaris* Menegh. appears to be a member of Prasiolaceae and possibly but a form of *Prasiola* (17).

The view that *Pleurococcus* is a reduced member of the Chaetophorales was first advanced by Chodat ((23) p. 616) and has been accepted by Oltmanns ((106) p. 304; cf. also (152)). In cell-structure it stands nearer to Chaetophoraceae than to Trentepohliaceae, and *Iwanoffia*, as well as *Fritschiella* (p. 253), shows that the former family has terrestrial tendencies (cf. also *Pleurastrum* among the Gongrosireae).

Printz (122) includes in Pleurococcaceae a number of other genera which appear to have little else in common with *Pleurococcus* than that reproduction is effected solely by vegetative division. These forms (*Elakatothrix*, *Coccomyxa*, *Pseudotetraspora*, *Dispora*, etc.), in great part imperfectly known, are better regarded as Palmellaceae (cf. p. 128) that have acquired the power of vegetative division. If Pascher's interpretation of the latter process is correct, moreover, vegetative division would not be as sharply distinct from that characteristic of Volvocales and Chlorococcales as has hitherto been supposed.

THE STATUS OF THE CHAETOPHORALES

The green filamentous types belonging to the Chaetophorales are the only algal forms to which we can look for a clue to the origin of the higher plants, since they exhibit in their heterotrichous habit the highest stage reached in the evolution of the plant-body among the Green Algae. This habit affords scope for the development of both prostrate and upright types. A form like *Draparnaldia* shows the beginnings of the differentiation of a main axis in the latter, with greater specialisation appearing in *Draparnaldiopsis*. Further, there are very marked terrestrial tendencies in the order, the Trentepohliaceae comprising the most elaborate subaerial Algae that are known. The normally prostrate gametophyte and the erect radial sporophyte of the higher plants might well have originated from similar heterotrichous forms by the suppression of one or other system in either case (43, 46). In this connection it may be noted that among the Trentepohlieae the asexual sporangia are usually borne on projecting threads, while the probable gametangia are commonly confined to the prostrate system, and that there is some evidence for the relegation of the two types of reproductive organs to distinct individuals which may possibly even be dimorphic (cf. p. 278).

Unfortunately little is as yet known of the life-cycle of the Chaetophorales. It is established that reduction occurs in the zygote of *Coleochaete scutata*. Yet we may well ask whether all the members of this order are haploid or whether some have advanced to an homologous alternation, such as exists among the Ulvaceae and Cladophoraceae. Reich's data (124) as to the occurrence of reduction in the zygote of *Stigeoclonium* are altogether unconvincing. It is significant that the zygotes of the Chaetophoreae appear, in part at least, to show direct germination. It is also of some interest that Meyer (95) did not observe zoospores in his sexually reproducing plants of *Chaetonema*. An investigation of the life-cycle of the Chaetophoraceae, and especially of the Trentepohlieae, is much to be desired, and in the case of the latter it could probably nowhere be so well accomplished as in the Tropics.

The following is an epitome of the classification of the order underlying the previous account:

1. *Chaetophoraceae:*

(*a*) *Chaetophoreae:* Chaetophora, Draparnaldia, Draparnaldiopsis, Endoclonium, Fritschiella, Iwanoffia, Pilinia, Stigeoclonium.

(*b*) *Prostratae:* Aphanochaete, Bolbocoleon, Chaetonema, Chaetopeltis, Didymosporangium, Endoderma, Gonatoblaste, Ochlochaete, Pringsheimia, Protoderma, Pseudopringsheimia, Pseudulvella, Trichodiscus, Trichophilus, Ulvella.

(*c*) *Erectae:* Microthamnion, Raphidonema, Thamniochaete.

2. *Trentepohliaceae:*

(*a*) *Gongrosireae:* Chloroclonium, Chlorotylium, Endophyton, Gongrosira, Leptosira, Lochmium, Pleurastrum, Pseudendoclonium, Pseudodictyon, Sporocladus.

(*b*) *Gomontieae:* Gomontia, Tellamia.

(*c*) *Trentepohlieae:* Cephaleuros, Phycopeltis, Physolinum, Rhizothallus, Stomatochroon, Trentepohlia.

3. *Coleochaetaceae:* Coleochaete.

4. *Chaetosphaeridiaceae:* Chaetosphaeridium, Conochaete, Dicranochaete, Oligochaetophora.

5. *Pleurococcaceae:* Pleurococcus.

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Order VI. *OEDOGONIALES*

The Oedogoniales are a sharply circumscribed group showing but few points of affinity with other Chlorophyceae. Whatever the ancestry, no intermediate forms appear to have lasted to the present day. Like the Conjugales they are essentially a freshwater group, playing a very important rôle nearly all the world over in the algal vegetation of smaller waters; the peculiar *Oedocladium* (fig. 91 F) is, however, mainly terrestrial. This genus, together with *Oedogonium* and *Bulbochaete*, constitute the sole family, Oedogoniaceae.

VEGETATIVE STRUCTURE

Oedogonium consists of long unbranched threads (fig. 91 E), generally free-floating in the mature condition, but attached by a specially differentiated basal cell when young (fig. 91 D); in species inhabiting flowing water the basal attachment naturally persists. The cylindrical cells are sometimes slightly swollen at their upper ends. *Bulbochaete*, on the other hand, is richly branched, the branches being unilateral and those of successive axes arising on alternate sides. Each cell bears a long colourless hair with a bulbous base; the terminal cells have two such hairs (fig. 91 A). *Bulbochaete* is smaller than *Oedogonium* and generally attached. *Oedocladium* (6, 17 *a*, 31), most of the species of which inhabit damp mud or sandy loam, consists of a branched creeping filament which bears colourless rhizoids, with a few septa, on its lower side and erect, branched, green threads on its upper;

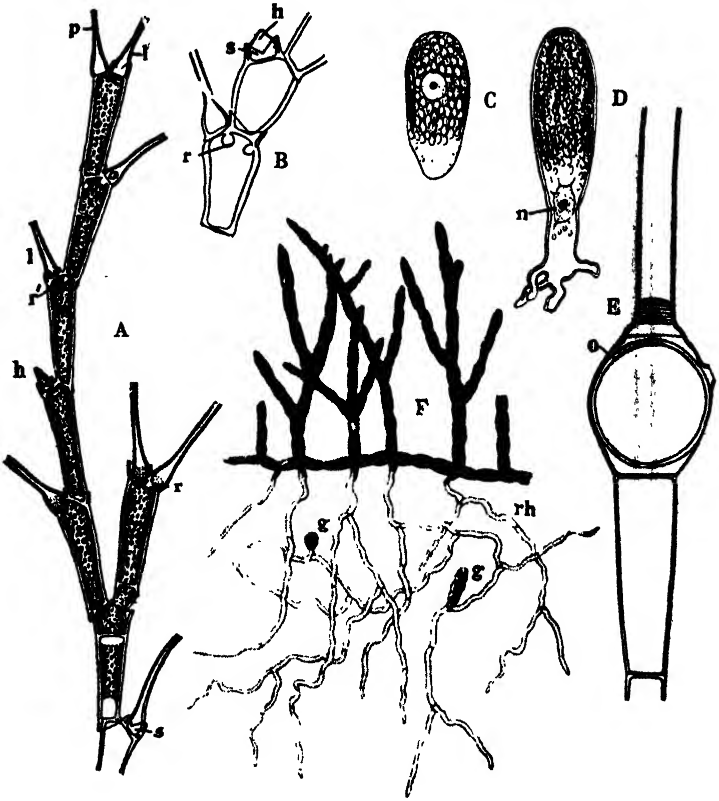

Fig. 91. Habits of Oedogoniales. A, *Bulbochaete setigera* Ag. B, *B. intermedia* De Bary, showing details of hair- and branch-formation. C, D, *Oedogonium concatenatum* Wittr., germinating zoospores. E, *O. lautumniarum* Wittr., with oogonium (*o*). F, *Oedocladium protonema* Stahl, prostrate thread, erect system, and rhizoids, the latter with two gemmae (*g*). *h*, hair-cell; *l*, mature hairs; *n*, nucleus; *p*, terminal hair; *r*, thickening ring; *r'*, thickening ring formed at point of branching; *rh*, rhizoid; *s*, sheath of hair. (A after Pringsheim; E after West; F after Stahl; the rest after Hirn.)

the rhizoids penetrate into the substratum (fig. 91 F). Lewis (cf. (29)) has described an aquatic species.

The cells in all cases contain a single, often large nucleus and an elaborate reticulate cylindrical chloroplast with narrow subparallel meshes and numerous scattered pyrenoids (fig. 92 G). It may vary from a greatly attenuated network to an almost entire cylinder, and there may be internal prolongations as in *Cladophora*.[1] The cell-wall is usually not conspicuously thickened and but scanty formation of mucilage occurs, except in *Bulbochaete* where the threads are often enveloped in mucilage which affords a home for Desmids, Diatoms, etc. According to Wisselingh (39) the cell-wall of *Oedogonium* consists of an inner cellulose layer and a surface investment (amyloid?).

One of the outstanding characteristics of the Oedogoniaceae lies in the peculiar method of growth of the cell-wall.[2] Some time prior to the division of a cell of *Oedogonium* a transverse ring of thickening appears at the upper end, just beneath the septum (fig. 92 A, D, *r*); in optical section the fully developed ring (fig. 92 B, C) is seen to consist of a central portion and, adjoining the protoplast, of a firmer bounding layer which is intimately concrescent with the inner layer of the cell-wall above and below the ring and extends a short distance into it (fig. 92 C). According to Wisselingh (39) the ring consists of cellulose intermingled with another substance that readily swells in various reagents and according to Steinecke (32) this is amyloid; cellulose is not present in the young ring and is most abundant in the firmer portion adjoining the protoplast. Wisselingh believes that the ring arises by intussusception.

Nuclear division is followed by the formation, across the middle of the cell, of a septum (*t*)[3] which, however, for some time remains unconnected with the longitudinal walls (fig. 92 D). Soon after, the cell-membrane breaks across transversely at the level of the ring and the latter gradually becomes stretched (fig. 92 E) to form a new cylindrical piece, intercalated between the parts (cap (*c*) and sheath (*s*)) of the old wall (fig. 92 E, F); simultaneously the septum (*t*) becomes displaced upwards till it takes up a permanent position near the edge of the lower part of the ruptured wall. The upper of the two daughter-cells has a wall formed mainly from the stretched thickening ring, but at its top there is a slightly projecting "cap" (*c*) constituted by the small part of the original membrane left above the point of rupture; the lower cell is almost entirely encased in the "sheath" (*s*)

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[1] According to unpublished observations of Dr N. Carter on an undetermined species of *Oedogonium*.

[2] See (1), (14), (19), (26), (33), (37), (39).

[3] Smith ((29) p. 438) is of the opinion that no septum-formation takes place at this stage, but merely a separation of the protoplast into two. The earlier investigators, however, all speak of a definite cellulose septum (cf. especially (33) p. 348).

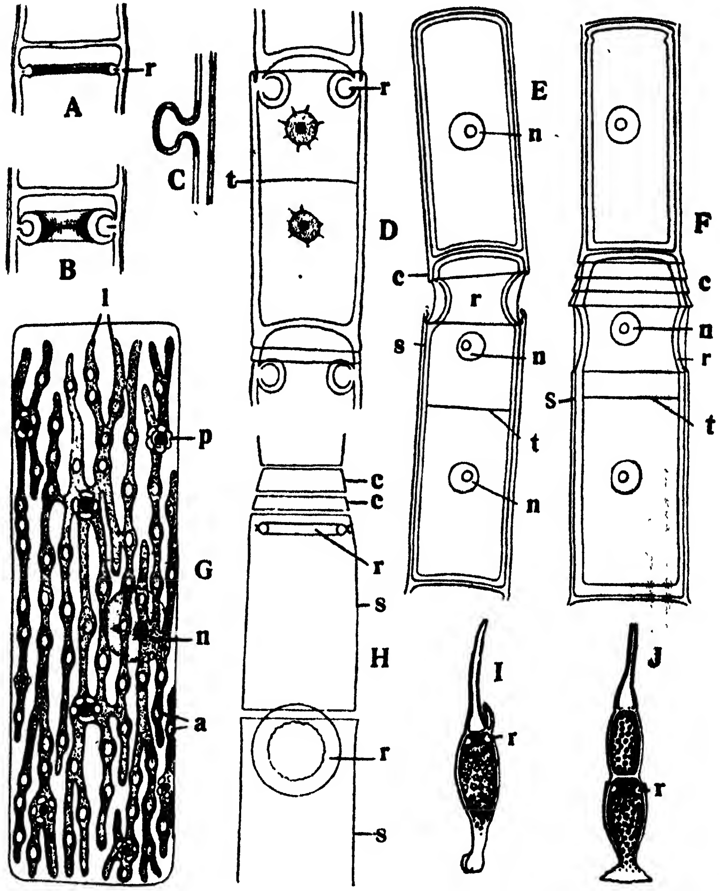

Fig. 92. Structure and mode of growth of *Oedogonium*. A, B, *O. tumidulum* Kütz., young and old thickening rings. C, E, F, H, *Oedogonium* sp.; C, thickening ring in optical section; E, F, successive stages in cell-division; H, cell treated with chromic acid, showing the diverse segments of the membrane. D, *O. Borisianum* Wittr., septum-formation following on nuclear division; the ring has not yet undergone stretching. G, cell-structure. I, J, *Bulbochaete setigera* Ag., early development of young plant. *a*, starch-grains; *c*, caps; *n*, nucleus; *p*, pyrenoid; *r*, thickening ring; *s*, sheath; *t*, septum. (A, B after Strasburger; D after Hirn; G after Schmitz; I, J after Pringsheim; the rest after Wisselingh.)

formed by the lower part of the old cell-membrane. "Cap-cells" usually divide repeatedly, exhibiting as many caps as there have been divisions (fig. 92 F, *c*), and the presence of such cells is a safe criterion for the recognition of a species of *Oedogonium*. In most cases (cf. however p. 301) the young plant derived from a zoospore divides after this manner from the first.

In *Oedogonium* growth is intercalary, cap-cells arising at variable intervals in the course of the threads, but in many species of *Bulbochaete* it is strictly basal and not more than one cap is generally formed on a cell (14, 26); in some of the species with elliptical oospores, however, intercalary growth occurs as well. In the unicellular plant developed from a zoospore of *Bulbochaete* a small colourless hemispherical cell is cut off apically by an ordinary septum; the wall of this cell is ruptured and turned to one side like a lid while the contents, secreting a new membrane, grow out as the first hair (fig. 92 I). The cell below develops a thickening ring (*r*) at its upper end and divides as above described for *Oedogonium*; the lower cell thus produced sooner or later forms a thickening ring (fig. 92 J) and divides, and thus a multicellular main axis originates in which the oldest cell is at the top and the youngest next to the basal cell.

Each cell, after its formation, grows out slightly at its apex towards one side or the other, and this protrusion is cut off as a colourless cell; its contents lengthen into a hair as in the one-celled germling, the ruptured wall forming an irregular sheath around the base (fig. 91 A, B, *s*). The terminal cell therefore bears two, the other cells one hair each. Each cell of a *Bulbochaete* thus has a plane base, whilst the upper end is composed of two sloping surfaces forming an obtuse angle with one another, the one bearing a hair, the other the next cell of the thread (cf. fig. 91 A). At more or less numerous points rings of thickening are formed below the septa which cut off the hairs (fig. 91 A, *r'*); the ensuing division leads to the cutting off of a lateral cell, the first one of a branch which likewise exhibits basal growth. In *Oedocladium* growth of the erect threads is apical (31) (cf. fig. 93 B), but there is a tendency for the caps to drop off after some time.

The peculiar method of cell-enlargement thus found in all Oedogoniaceae finds a slight parallel in the early growth of the young plants of some species of *Microspora*, but there are marked differences; Steinecke (32 *a*) also compares it with that of *Trentepohlia*. Freund (8) has investigated the growth of *Oedogonium* in relation to external conditions; a deficiency of nutritive salts leads to a cessation of cell-division, the cells lengthening and becoming filled with reserves.

VEGETATIVE AND ASEXUAL REPRODUCTION

Apart from the usual fragmentation, prolific reproduction takes place by means of large multiflagellate zoospores, always produced singly from the ordinary cells.[1] According to Gussewa (11, 12) zoospore-development depends on the presence of a certain amount of free carbon dioxide in the surrounding water (cf. also (7), (17)). The differentiation of the zoospores takes place rapidly and the stages are readily followed. A slight contraction of the protoplast is succeeded by the movement of the nucleus towards one side of the cell (cf. fig. 6 D, p. 30) where a colourless area appears (fig. 93 D). Around its base in stained preparations blepharoplasts are seen to differentiate (fig. 6 E), and the arising flagella become visible as fine striae (fig. 6 F), while an eye-spot is often to be recognised. Soon the cell-wall ruptures near its upper end, the two halves gape apart, and the zoospore slowly glides out (fig. 93 E). At the moment of liberation it is enveloped by a delicate mucilage-vesicle (fig. 93 F, *v*), but this soon vanishes. According to Steinecke (32) the protoplast of the cell developing a zoospore secretes mucilage at either end, while at the level of the future point of rupture the cellulose-wall becomes converted into amyloid.

The zoospores (fig. 93 G, I) are almost spherical or pear-shaped and deep green, but there is a well-marked colourless beak around the base of which the usually short flagella arise. According to Kretschmer ((20); cf. also (21) p. 491, (22) pp. 184, 189) there are two rings of basal granules giving origin to the flagella (fig. 6 K, p. 30), while in *O. capillare* Gussewa (12) describes a single ring-shaped blepharoplast (fig. 93 I, J). An eye-spot is, according to Mainx (21), always present. In most cases it is the anterior end of the zoospore that becomes adpressed to the substratum and that develops into the often richly lobed holdfast (9, 25, 38) by means of which attachment is effected (fig. 91 D). In some species of *Oedogonium*, however, the zoospores flatten out laterally against the substratum and form a hemispherical basal cell (28) from the convex surface of which a new thread gradually develops, the membrane of the basal cell at its point of origin becoming turned to one side like a lid (fig. 93 C).

In *Oedocladium* (31) vegetative multiplication by means of short rows of two, three, or more cells, filled with oil and starch and acquiring red-coloured contents (akinetes), also occasionally occurs (fig. 93 B). Similar rows of akinetes are more usually formed on the subterranean rhizoids (fig. 91 F, *g*). Wille (36) has recorded resting cells in some species of *Oedogonium*.[2]

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[1] See (1), (5), (12), (21), (26), (33), (34).

[2] Handa's record (13) of such stages is open to doubt, as the presence of a parasite is to be suspected.

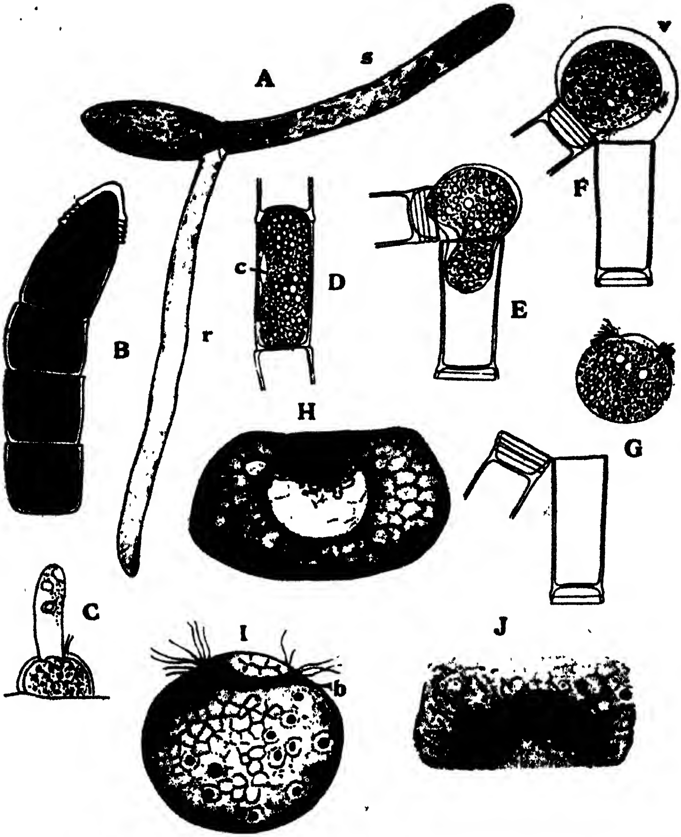

Fig. 93. Asexual reproduction of Oedogoniales. A, B, *Oedocladium protonema* (after Stahl); A, young plant arising from zoospore; B, akinetes from end of an erect thread. C, *Oedogonium rufescens* Wittr. (after Scherffel), germling with hemispherical basal cell. D–G, *O. concatenatum* (after Hirn), stages in formation and liberation of zoospore. H–J, *O. capillare* Kütz. (after Gussewa); H, oospore, nucleus in synapsis; I, zoospore with annular blepharoplast (*b*); J, surface-view of same. *c*, colourless area; *r*, rhizoid; *s*, young thread; *v*, vesicle.

SEXUAL REPRODUCTION

Sexual reproduction, which appears to take place readily in many species of *Oedogonium*, though not so frequently in *Bulbochaete*, is of an advanced oogamous type.[1] According to Mainx ((21) p. 500) it only sets in when the material has acquired a certain sexual tonus and the external conditions are suitable; of these the most important is a hydrogen-ion concentration on the alkaline side, generally somewhat lower than that which admits of an optimum vegetative development. Nitrogen-deficiency is also essential (12).

Oogonia and antheridia are produced on the same plant in some (*macrandrous*) species of *Oedogonium* and *Bulbochaete*, as well as in most species of *Oedocladium* (17 a, 31). In *Oedogonium Kurzii* Spessard (30) finds that the antheridia appear a day later than the oogonia, so that cross-fertilisation is probable. The majority of the dioecious species exhibit a curious dimorphism of the sexual plants (*nannandrous* species), the oogonia being produced in the ordinary threads, the antheridia in special "dwarf-males" consisting at the best of only a few cells. It is now known that this habit is found also in a species of *Oedocladium* (*O. hazenii* Lewis (29)).

These dwarf-males originate from a special type of swarmer called an *androspore*, produced singly within flat discoid cells (androsporangia) formed by repeated transverse division of the ordinary cells (fig. 94 B). These androsporangia occur either in the same filaments as the oogonia or in distinct ones. The androspores are smaller than the zoospores and sometimes yellowish in colour, but otherwise show the same characteristics (fig. 94 B). At the end of their brief swarming period they settle down either on an oogonium or on one of the adjacent cells and germinate to produce a minute plant which develops a rhizoid-like elongate attaching cell[2] and very soon proceeds to form one or more flat antheridia (figs. 94 E, 95 B). In a few species of *Oedogonium* the dwarf-male consists only of the attaching cell (fig. 94 A) which produces two spermatozoids from its contents, while in some *Bulbochaetes* the terminal cell may produce a normal hair.

The antheridia are flat cells resembling the androsporangia and formed in the same way (fig. 94 C, D). The number of consecutive antheridia is variable. In most cases the contents of each antheridium divide (22) to form two spermatozoids which usually lie side by side (fig. 94 F, *s*), though superposed in the antheridia of the dwarf-males (fig. 95 D); the production of only one spermatozoid is rare. The sperms are usually described as resembling miniature pale green or yellowish zoospores (fig. 94 G), but in *Oedogonium Kurzii* Spessard (30)

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[1] See (1), (14), (15–17), (26).

[2] Only very rarely are there other vegetative cells ((14) p. 24).

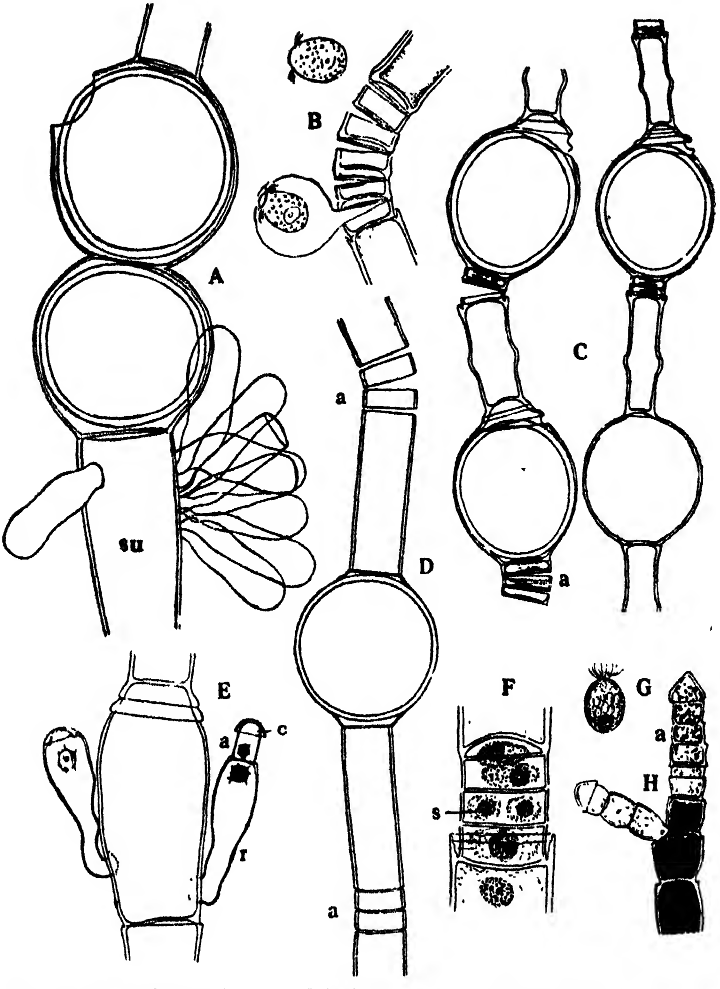

Fig. 94. Sexual reproduction of Oedogoniales. A, *Oedogonium cyathigerum* Wittr., with two oogonia and many unicellular dwarf-males on the supporting cell. B, *O. Braunii* Kütz., liberation of androspores. C, *O. nodulosum* Wittr. var. *commune* Hirn, monoecious threads. D, *O. zigzag* Cl. var. *robustum* West, the same. E, *O. concatenatum*, oogonium with dwarf-males. F, G, *O. Boscii* Wittr.; F, antheridia with young spermatozoids; G, spermatozoid. H, *Oedocladium protonema*, young antheridia. *a*, antheridia; *c*, cap; *r*, rhizoid; *s*, spermatozoid; *su*, supporting cell. (A, D after West; F, G after Klebahn; H after Stahl; the rest after Hirn.)

found that they showed signs of dorsiventrality, possessed contractile vacuoles, and exhibited a different type of movement. The spermatozoids are liberated in the same way as the zoospores and androspores (cf. fig. 94 B). The antheridia of the dwarf-males are either cut off by a simple septum or more commonly with the customary ring-formation, in which case the antheridium is covered by the cap (fig. 94 E, *c*).

The oogonia in the vast majority of cases are prominently enlarged cells, usually spherical or ellipsoidal in shape (figs. 94 A, C, 95 B). In *Oedogonium* and *Oedocladium* (fig. 95 I) they are formed by a single division of a cap-cell, the upper segment during the stretching of the thickening ring undergoing more or less distension to form the oogonium; the underlying sheath-cell, known as the *supporting cell*, is often rather poor in contents, but may in some species undergo further segmentation to form rows of two (fig. 94 A), three, or even more oogonia. In some cases (e.g. *Oedogonium Borisianum* (Le Cl.) Wittr.) it is appreciably swollen. According to Ohashi (22) there is no supporting cell in *O. americanum*.

In *Bulbochaete* two divisions are involved in the production of an oogonium which consequently has two supporting cells (14, 26). After the first division the septum becomes fixed at the middle of the sheath (fig. 95 C), so that the membrane of the upper segment is formed by a short cylindrical piece of the sheath and above that by the stretched thickening ring which is becoming bulged out to form the oogonium. A second ring then develops in the median region of the young oogonium, followed by a transverse rupture of the wall at this point; the septum formed in connection with this second division lies on a level with the top of the first-formed sheath, so that both supporting cells (fig. 95 D, *1*, *2*) are included in the latter. This curious development is responsible for the fact that the wall of the mature *Bulbochaete* oogonium can nearly always be seen to consist of three pieces (fig. 95 B).[1]

The contents of the oogonium contract to form a single ovum which, opposite the point of opening, exhibits a well-marked colourless receptive spot (fig. 95 G, *r*). Except in a certain number of the species of *Oedogonium* the oogonia open by a small pore formed by the gelatinisation of the tip of a papilla (fig. 95 E, G). In *Oedogonium*, however, opening is not uncommonly effected by a transverse split in the wall (26), while a thin membrane deposited on the inner side of the latter forms a definitely shaped conduit with a more or less circular aperture leading down to the ovum. It appears that such an internal membrane is formed in all cases, even where the oogonium opens by a pore ((14) p. 8) (fig. 95 F, *m*). In the few cases in which the life-history has been studied the extrusion of a small quantity of

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[1] The two closely apposed lines in the middle of the oogonium in fig. 95 B and D belong to the oospore-membrane.

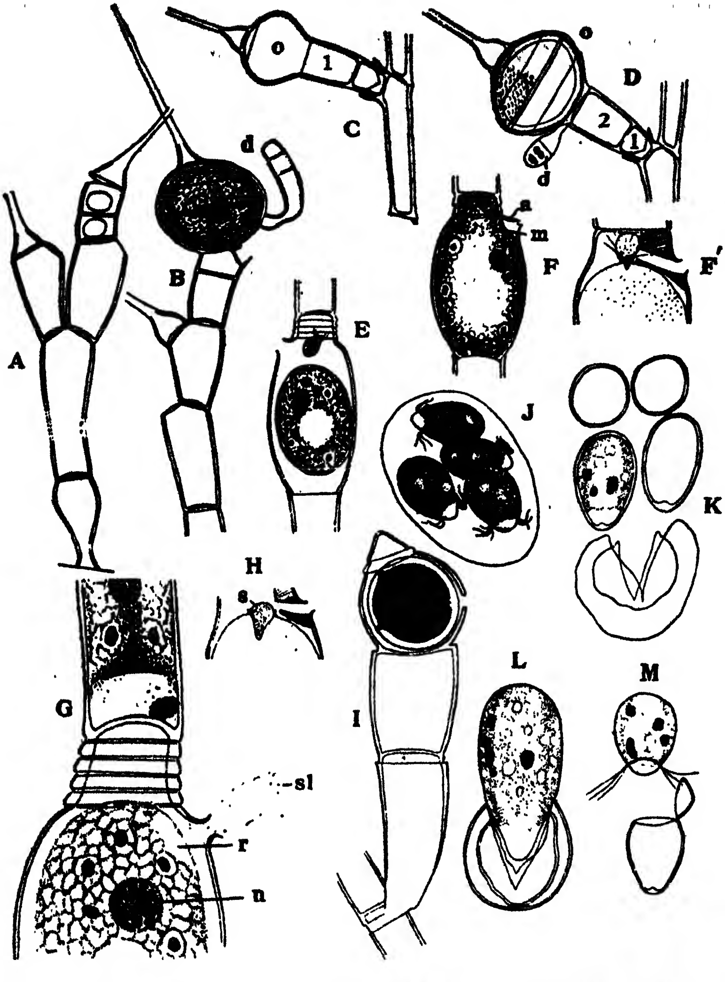

Fig. 95. Sexual reproduction of Oedogoniales. A, B, *Bulbochaete gigantea* Pringsh. C, D, *B. Brebissonii* Kütz., two stages in development of oogonium. E–G, *Oedogonium Boscii*; E, fertilised oogonium with supernumerary spermatozoid; F, mature oogonium; G, part of same enlarged. F′, H, *O. Kurzii* Zeller, successive stages in fertilisation. I, *Oedocladium protonema*, thread with oogonium. J, *Oedogonium pluviale* Nordst., germinating oospore. K–M, *Oedogonium* sp., germination of oospore; K, normal germination; L, abnormal germination, with production of a single large individual; M, liberation of swarmer from one member of a normal tetrad. *a*, aperture of oogonium; *d*, dwarf-male; *m*, inner membrane of oogonium; *n*, nucleus; *o*, oogonium; *r*, receptive spot; *s*, spermatozoid; *sl*, mucilage. (A, F after Tiffany; E–G after Klebahn; F′, H after Spessard; I after Stahl; J after Juranyi; K–M after Mainx; the rest after Hirn.)

mucilage from the mature ovum has been observed (cf. fig. 95 G, *sl*). The process of fertilisation (fig. 95 F′, H) has been studied by

The oospores develop a thick, usually three-layered membrane and the contents often assume a red colour; in some cases they appear to be able to germinate directly, but in others (12, 21) a prolonged resting period is necessary. Mainx, moreover, found that optimum germination only occurs if the oospores have been subjected to frost. At the commencement of germination[1] the oospores lose their pronounced red colour and soon after the contents divide into four parts. It appears that in some species this division takes place within the still intact zygote-membrane, whilst in others the naked contents of the zygote are liberated into a vesicle and there divide; in the former case the products of division are likewise set free and remain for a time enveloped by a bladder (fig. 95 J). Ordinarily the naked protoplasts soon develop flagella and escape as swarmers through a definite aperture formed in the enveloping vesicle, but under certain conditions aplanospore-formation takes place; these aplanospores are set free by gelatinisation of the enveloping vesicle (fig. 95 K) and, after some days, liberate swarmers (fig. 95 M) ((21) p. 509). The swarmers in all cases give rise to new plants.

Gussewa (12) has shown that reduction occurs during the germination of the zygote in the case of *Oedogonium capillare* (cf. fig. 93 H), so that the Oedogoniaceae are haploid, as had long been taken for granted. Some of the four nuclei may degenerate, in which case less than four swarmers result. Mainx has established in the case of *O. plagiostomum* var. *gracilius* that two of the swarmers give rise to male and two to female plants, and no doubt this will be found to be general in the dioecious species.

Parthenogenesis, recorded already by earlier investigators, is, according to Mainx (21), not uncommon; in *O. capillare* in such cases the oogonia develop no aperture (12). Of special interest are those instances, observed by Mainx ((21) p. 516), in which the zygotes give rise to a single, presumably diploid swarmer (fig. 95 L) of large size.[2] These swarmers develop into threads of twice the normal width which are always female, though their oogonia are much flatter than those of normal female threads and, moreover, are formed in long series, in both respects recalling the antheridia. Mainx suggests that the female character is dominant, but that the recessive character of the male finds expression in the special features presented by the oogonia. The ova of such plants are capable of fertilisation by normal haploid spermatozoids, but the further fate of the presumably triploid zygotes is unknown.

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[1] See (4), (12), (15), (21), (26).

[2] Cf. the analogous cases among Volvocales discussed on p. 119.

THE STATUS OF THE OEDOGONIALES

Among many peculiarities the most striking feature of the Oedogoniales are no doubt the dwarf-males. In several dioecious macrandrous species of *Oedogonium* the male threads are narrower than the female, and there is an occasional tendency for the young plants of this genus arising from zoospores to develop antheridia precociously (9, 35). Such cases may indicate the way in which this habit has arisen. The androspores have, however, also been regarded as prematurely liberated sperm mother-cells ((23) p. 340, (27)) and, in the case of *O. diplandrum* (15) where the dwarf-males are unicellular, their division would only be deferred by the intervening swarming period. The great similarity between the androsporangia and the antheridia lends some further support to this view (cf. also (29) p. 445).

Pascher (24) has, however, pointed out the close analogy between the dwarf-males and the dwarf individuals produced by swarmers intermediate between the normal types in the Chaetophoreae. He suggests that the species possessing such dwarf-males are to be regarded as the more primitive, since they have three types of swarmers of which the intermediate ones, representing zoospores which have lost the full power of vegetative development, in this case give rise to dwarf individuals producing male cells. In the course of further development the protoplast of the androsporangium became sexually modified in such a way that it acquired the capacity of producing male cells directly. The macrandrous species on this view are to be looked upon as more specialised than the nannandrous ones. On the whole the view that regards the androspores as prematurely liberated sperm mother-cells appears to have most to commend it (cf. also (18) p. 119).

Bohlin ((3) p. 35) first applied the designation Stephanokontae to the Oedogoniales, implying a distinct origin for this order from a flagellate stock having a crown of flagella, although he included the order as a subdivision of Chlorophyceae. Blackman and Tansley (2), however, raised the Stephanokontae to the rank of a separate class, and this has been followed by many subsequent authors. A separation of the Oedogoniales from the rest of the Green Algae must, however, obscure the essential principles underlying the present-day concept of algal evolution, since in the pigmentation of their chloroplasts, in the possession of pyrenoids with a starch-sheath, in the storage of starch, and the chemical nature of their membranes they are altogether of the same type as other Green Algae (10). Nor do they stand more isolated from the bulk of the latter than do many recognised families of this class (e.g. Coleochaetaceae).

Even if such special characteristics as the dwarf-males and the peculiar mode of growth of the cell-wall be left on one side, the Oedogoniales present few points of contact with other filamentous

Chlorophyceae. The large zoöspores, the elaborate chloroplast, and the complex female organs are almost as peculiar and, although some authorities have compared the Oedogoniales with *Cylindrocapsa*, the resemblances on closer scrutiny appear superficial. Pascher ((24) p. 277) sees some relationship to Chaetophorales in the ring-shaped chloroplast, in the production of hairs,[1] in the branched threads of two of the genera, and in the dwarf-males (cf. above). To these points of contact we may add the heterotrichous habit of *Oedocladium* and certain resemblances in the mode of growth of the cell-wall in species of *Trentepohlia* with divergent strata. These various resemblances may imply an origin of Oedogoniales from a common ancestry with Chaetophorales.

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[1] Even in *Oedogonium* some species have threads terminating in hairs.

en art af slaegten *Oedogonium*.' *Bot. Tidsskr.* III, **2**, 1–15, 1877. **26.** Pringsheim, N. 'Morphologie der Oedogonien.' *Jahrb. wiss. Bot.* **1**, 1–81, 1858. **27.** Schaffner, J. H. 'Extraordinary sexual phenomena in plants.' *Bull. Torrey Bot. Club*, **54**, 619–29, 1927. **28.** Scherffel, A. 'Einige Beobachtungen über Oedogonien mit halbkugeliger Fusszelle.' *Ber. Deutsch. Bot. Ges.* **19**, 557–63, 1901. **29.** See No. 86 on p. 228 (Smith, 1933). **30.** Spessard, E. A. 'Fertilization in a living *Oedogonium*.' *Bot. Gaz.* **89**, 385–93, 1930. **31.** Stahl, E. '*Oedocladium protonema*, eine neue Oedogoniaceen-Gattung.' *Jahrb. wiss. Bot.* **23**, 339–48, 1892. **32.** Steinecke, F. 'Hemizellulosen bei *Oedogonium*.' *Bot. Archiv*, **24**, 391–403, 1929. **32*a*.** See No. 144 on p. 295 (Steinecke, 1929). **33.** See No. 69 on p. 248 (Strasburger, 1880). **34.** See No. 175 on p. 58 (Strasburger, 1900). **35.** West, G. S. 'Observations upon two species of *Oedogonium*, with some remarks upon the origin of the dwarf males.' *Journ. Bot.* **50**, 321–5, 1912. **36.** Wille, N. 'Ueber Akineten und Aplanosporen bei den Algen.' *Bot. Centralbl.* **16**, 215–19, 1883. **37.** Wille, N. 'Ueber die Zellteilung bei *Oedogonium*.' *Jahrb. wiss. Bot.* **18**, 443–54, 1887. **38.** Wille, N. 'Ueber das Keimen der Schwärmsporen bei *Oedogonium*.' *Ibid.* **18**, 454–8, 1887. **39.** Wisselingh, C. v. 'Ueber den Ring und die Zellwand bei *Oedogonium*.' *Beih. Bot. Centralbl.* **23**, 1, 157–90, 1908.

Order VII. *CONJUGALES*

The Conjugales are a well-defined group and very little experience is necessary to recognise one of its members, characterised as they are by the usual marked symmetry of the cell and an elaboration of the chloroplasts unparalleled in any other series of Green Algae. In the vast majority of cases the chloroplasts are axile, and it is probable that this in all cases represents the original condition. Apart from these features which distinguish the vegetative phases, the Conjugales are further distinguished by the complete absence of motile reproductive elements and by the occurrence of a special type of sexual process in which a fusion of amoeboid gametes is involved and which is usually spoken of as *conjugation*. In the vast majority of cases the gametes are the undivided protoplasts of ordinary vegetative cells. Otherwise reproduction is effected only by cell-division. There are no truly marine forms.

Included in the order are two somewhat different types, viz. the Zygnemoideae in which the vegetative body consists of an unbranched filament, and the Desmids in which the habit is prevalently unicellular. The latter, however, comprise two series of forms whose relation to one another is by no means clear (108, 109, 185). In the one series, the Saccoderm Desmids (*Mesotaenium*, *Cylindrocystis*, *Spirotaenia*, etc., cf. fig. 96), the cell-wall is composed of a single piece, is devoid of pores, and is usually (not in *Spirotaenia*) readily soluble in ammoniated copper oxide. In the Placoderm Desmids, on the other hand, the cell-wall consists of two (rarely more) pieces, is generally traversed by pores, and is differentiated into two layers of which the outer is little soluble in ammoniated copper oxide. There are other differences between these two groups of Desmids which are not so sharply defined. Thus, in the Saccodermae the chloroplasts are usually of a less elaborate type than in the Placodermae, and there is a tendency for the zygote on germination to give rise to four individuals rather than to the two customary in the Placodermae.

A fairly close affinity between the Saccoderm Desmids and the Zygnemoideae is apparent, but the relation of the highly specialised Placodermae to the others is by no means evident. There is no indication of how the complex wall-structure of the latter has been arrived at, and the possibility of an origin distinct from that of the other two groups must be envisaged. One cannot feel sure that the undoubted resemblances are not due to homoplasy. It is therefore difficult to endorse the views, either of West ((178) p. 80, (179) p. 331) and Lütkemüller (107) as to the close relation of Saccoderm and Placoderm Desmids, or those of Oltmanns ((125) p. 126) who regards the former as descended from the ancestral type from which both the Zygnemoideae and the Placoderm Desmids originated along separate lines. A clearer conception of the Conjugales is probably obtained by grouping the Saccoderm Desmids (Mesotaenioideae) and the Zygnemoideae as Euconjugatae and regarding the Placoderm Desmids as a separate suborder. A similar attitude has recently been adopted by Pascher ((130); cf. also (42) p. 32).

Suborder I. *EUCONJUGATAE*

(*a*) THE MESOTAENIOIDEAE (SACCODERM DESMIDS)

The "Desmids" here included form a single family, the Mesotaeniaceae, whose cell-structure is relatively simple and which are probably primitively unicellular; the principal genera are *Mesotaenium* (fig. 96 A), *Roya* (fig. 96 E), *Cylindrocystis* (fig. 96 B), *Spirotaenia* (fig. 96 C, D), and *Netrium* (fig. 96 F). Alone in *Ancylonema Nordenskiöldii* (9, 123) are the individuals united to form short threads. The cells are commonly rod-shaped or oblong and without a median constriction, such as occurs so commonly in the Desmids proper; the cross-section is invariably circular. The smooth cell-wall is composed of a single piece and there is no evidence, direct or indirect, of the presence of pores, nor is there any differentiated outer layer. According to Pothoff (136) the membrane of *Spirotaenia condensata* is composed of mucilage only.

The often prolific multiplication takes place by the formation of a transverse septum approximately across the middle of the cell; this

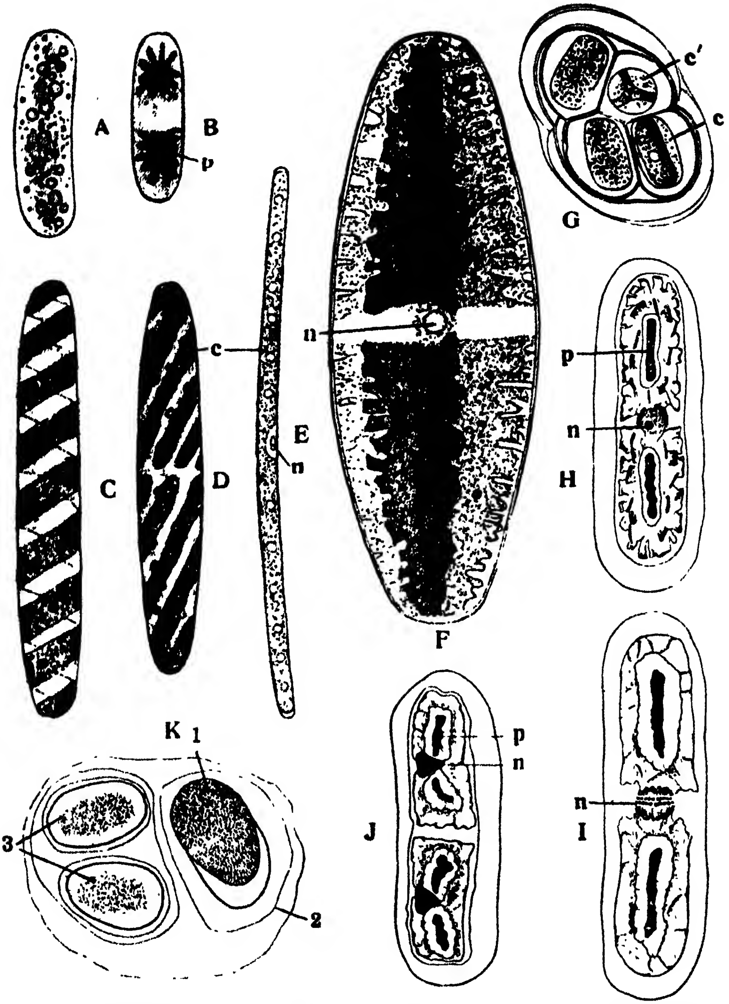

Fig. 96. Mesotaenioideae. A, *Mesotaenium De Greyi* Turn. B, *Cylindrocystis Brebissonii* Menegh. C, *Spirotaenia condensata* Bréb. D, *S. obscura* Ralfs. E, *Roya cambrica* West. F, *Netrium Digitus* (Ehrenb.) Itzigs. & Rothe. G, *Mesotaenium macrococcum* (Kütz.) Roy et Biss., palmelloid colony. H–J, *Cylindrocystis Brebissonii*; H, cell-structure; I, J, two stages in division, in I the nucleus in mitosis. K, *C. crassa* De Bary, division in three directions (*1*, *2*, *3*, cells in successive planes). *c*, chloroplast (*c'*, end-view of same); *n*, nucleus; *p*, pyrenoid. (G after De Bary; H–J after Kauffmann; K after Puymaly; the rest after West.)

septum arises as an annular ingrowth from the longitudinal walls and, by the subsequent dissolution of the middle lamella, the two daughter-cells separate from one another. A detailed study of this division has been made in *Cylindrocystis* by Kauffmann (83). According to him a great elongation of chloroplast and pyrenoid in each half of the cell precedes the division of the nucleus (fig. 96 H, I), and, while the latter process is proceeding, each pyrenoid and chloroplast gradually divides into two, so that the two pairs of chloroplasts of the daughter-cells are formed before the separating septum is produced (fig. 96 J). According to West growth of the daughter-cells takes place at the newly formed pole ((179) p. 363), but this requires further investigation.

Several of the species of *Mesotaenium* and *Cylindrocystis*, inhabiting terrestrial substrata, exhibit large numbers of individuals within a common mucilage-envelope which not uncommonly shows distinct strata representing the gelatinised outer layers of the membranes of successive generations (fig. 96 G). Puymaly (141) has drawn attention to the fact that, in *Cylindrocystis crassa*, division takes place in two or three successive planes at right angles to one another (fig. 96 K). This marks a more primitive condition than that encountered in Placoderm Desmids, where division always takes place in the transverse plane only, and the question of its occurrence in other Mesotaeniaceae is worthy of investigation.

The genera of this family present us with the three types of chloroplast-structure found in the cells of Zygnemoideae, viz. a flat axile plate[1] with one or several pyrenoids in *Mesotaenium* (fig. 96 A, G), a pair of stellate axile chloroplasts each with a massive central pyrenoid in *Cylindrocystis* (fig. 96 B), and a parietal spiral band twisting to the left with irregularly scattered pyrenoids in several species of *Spirotaenia*[2] (106) (fig. 96 C). Some species of the latter, however, have an axile chloroplast with a variable number of spirally twisted ridges (fig. 96 D), and this possibly represents the original type within the genus. In *Ancylonema* the chloroplast is a narrow and twisted parietal plate with a single pyrenoid. *Netrium* (fig. 96 F) has two axile chloroplasts, more like those of the Desmids proper and consisting of a central rod with a considerable number of radiating longitudinal plates, usually deeply notched along their free edges; each chloroplast generally contains one much elongated pyrenoid. This type may well have been derived from that of *Cylindrocystis* by elongation. *Roya* (fig. 96 E), whose cells show great similarity to those of some species of *Closterium*, has a single axile chloroplast with a small number of longitudinal ridges and a median series of pyrenoids, although in older cells the chloroplast may be divided at the middle.

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[1] Rarely triradiate (cf. fig. 96 G, *c'*).

[2] Reverdin's *Closteriospira* ((143) p. 86), on account of its oblique division, cannot at present be definitely assigned to this group.

The cells in all cases contain a single central nucleus, which in *Mesotaenium* is adpressed to the chloroplast, while in *Roya* it is lodged in a small bay in the latter.

Sexual reproduction is of frequent occurrence in species of *Cylindrocystis* and *Mesotaenium* and is recorded in all genera except *Ancylonema*. In the first two genera (6, 83, 109) the conjugating cells, with their long axes parallel or at right angles to one another and usually embedded in mucilage, become joined by conjugation processes which meet end to end (fig. 97 A). In the case of *Netrium* Pothoff ((136) p. 668) finds that the processes arise at the point of contact of two apposed individuals which are gradually pushed apart as the processes lengthen (fig. 97 J); this, the usual method of conjugation in Zygnemoideae (p. 324), is likely to be of general occurrence in those Mesotaeniaceae that form a conjugation tube. By solution of the separating wall between the processes the conjugation canal is established and within this the contracted protoplasts meet and fuse; at the same time, in *Cylindrocystis* and *Mesotaenium*, a marked widening of the canal takes place, so that it is no longer sharply defined from the membranes of the conjugating cells (fig. 97 B). The zygote develops a thick several-layered wall and remains for a time at least surrounded by the joined membranes of the two gametes (fig. 97 C, K). The sexual process is altogether isogamous. According to Kauffmann (83) the nuclei in *Cylindrocystis* fuse soon after the protoplasts have amalgamated (fig. 97 D, E), but Pothoff (136) states that in other members of the family fusion only occurs after the resting period (cf. fig. 97 K).

In certain species of *Spirotaenia* (e.g. *S. condensata* (3)) the contents of the conjugating individuals divide into two prior to fusion (fig. 97 M), this being accompanied by a gradual gelatinisation of the wall until the four protoplasts are embedded in a common mass of structureless mucilage. Subsequently the corresponding half protoplasts fuse with the production of a pair of zygospores (fig. 97 N–P). Such double zygospores have also been recorded as an exception in *Cylindrocystis Brebissonii* (4, 185). No conjugation canals are formed in this case.

Two successive nuclear divisions, of which the first is the reduction division (83), occur in the germination of the zygospore after the usual resting period (fig. 97 F, G). It would appear to be the rule in the Mesotaeniaceae that four new individuals are constituted around these four nuclei (fig. 97 H, I), although only two are occasionally formed in *Spirotaenia* ((83) p. 765) and *Mesotaenium* (178). In *Cylindrocystis* the four chloroplasts of the gametes persist and are distributed to the offspring, but in *Spirotaenia*, according to Pothoff (136), one of the two chloroplasts disintegrates during the resting period. The new individuals are liberated by rupture of the zygospore membrane

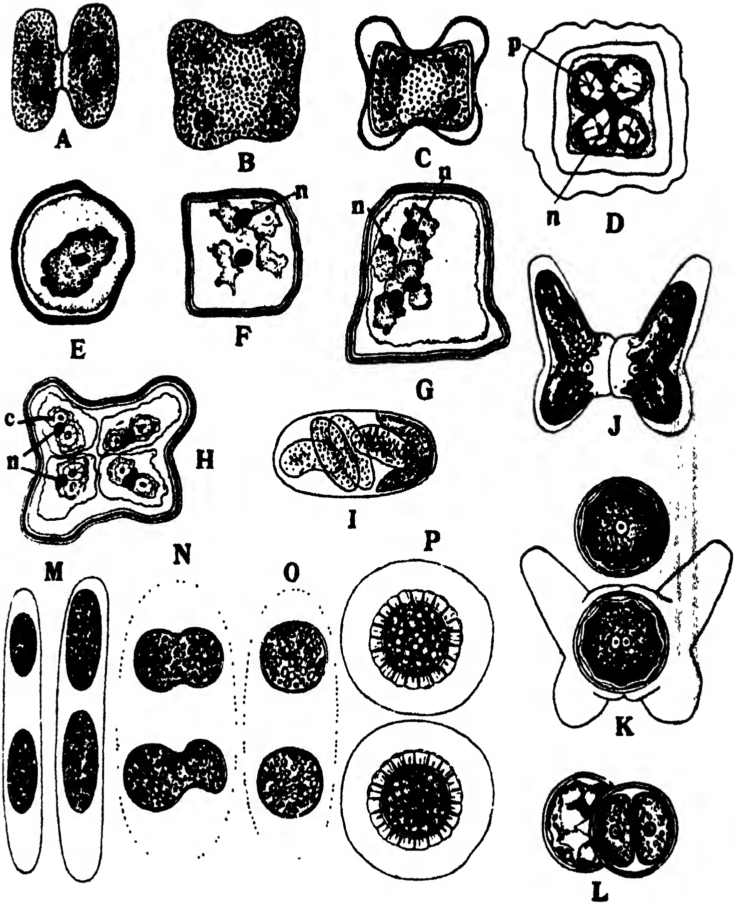

Fig. 97. Sexual reproduction of the Mesotaeniaceae. A–H, *Cylindrocystis Brebissonii* Menegh.; A–C, stages in conjugation; D, young zygote, nuclei in contact; E–H, stages in germination, F bi- and G quadrinucleate stages, H with four protoplasts. I, *Mesotaenium chlamydosporum* De Bary, liberation of new individuals. J–L, *Netrium Digitus* (diagrammatic); J, conjugation; K, zygote with two nuclei, above the same with nuclei fused just prior to germination; L, germination. M–P, *Spirotaenia condensata*, stages in conjugation of two individuals, production of two zygotes. *c*, chloroplast; *n*, nucleus; *p*, pyrenoid. (D–H after Kauffmann; J–L after Pothoff; M–P after Archer; the rest after De Bary.)

(fig. 97 I). *Netrium* ((136) p. 669) shows a closer approach to the true Desmids in producing only two new individuals (fig. 97 L), although four nuclei are formed in the zygote in the usual way.

Many of the Mesotaeniaceae occur in upland pools and peat bogs. As already mentioned, species of *Mesotaenium* and *Cylindrocystis* are not uncommon in terrestrial situations; two of these (*M. purpureum*, *M. violascens*) have purple-coloured cells due to the presence of phycoporphyrin in the sap. The same feature is seen in *Ancylonema Nordenskiöldii* which is a characteristic member of snow-floras (9). *Mesotaenium caldariorum* is able to utilise organic nutriment (38).

(*b*) THE ZYGNEMOIDEAE

VEGETATIVE STRUCTURE

The Zygnemoideae comprise a number of the commonest filamentous freshwater Algae, all of them normally unbranched, although in *Zygnema* and *Mougeotia* (fig. 98 K) short few-celled laterals are very occasionally observed (129, 184). The Zygnemoideae favour more particularly smaller stagnant pieces of water, but a few are found attached in the littoral zone of lakes (*Spirogyra adnata*, etc.) and in flowing water. They appear to be essentially autotrophic (38).[1] They are specially abundant in the spring months, generally occurring as bright green free-floating masses, but some kind of attaching organ is present in young stages in several genera. These attaching cells, especially in forms growing in moving water, may often be branched or elaborately lobed[2] (fig. 98 I, N, O). Otherwise there is no differentiation among the cylindrical cells. Planktonic species of *Mougeotia* often have twisted or spirally coiled threads (187). A small number of species are adapted to a terrestrial mode of life (140), and of these *Zygogonium ericetorum* (56) is very widely distributed. Only very rarely are members of this series found in saline waters (78 *a*).

The chloroplasts are essentially of the same three types as were noted in the Mesotaeniaceae, viz. a flat axile plate with several pyrenoids (*Mougeotia*, fig. 98 A, B; *Debarya*; *Gonatonema*, etc.), a pair of axile stellate chloroplasts each with a large central pyrenoid and often showing peripheral enlargement of the radiating processes (*Zygnema*, fig. 98 C, J; *Pyxispora*), or one or more parietal spiral bands twisting to the left (*Genicularia*, fig. 98 M) or right (*Spirogyra*, fig. 98 H; *Sirogonium*); in one species of *Debarya* pyrenoids are sometimes lacking (128). The more complex type of *Netrium* and *Roya* is not represented in this series.

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[1] The older work (cf. (14)) cannot be regarded as reliable in the light of modern investigation.

[2] See (15), (45), (47), (79), (129).

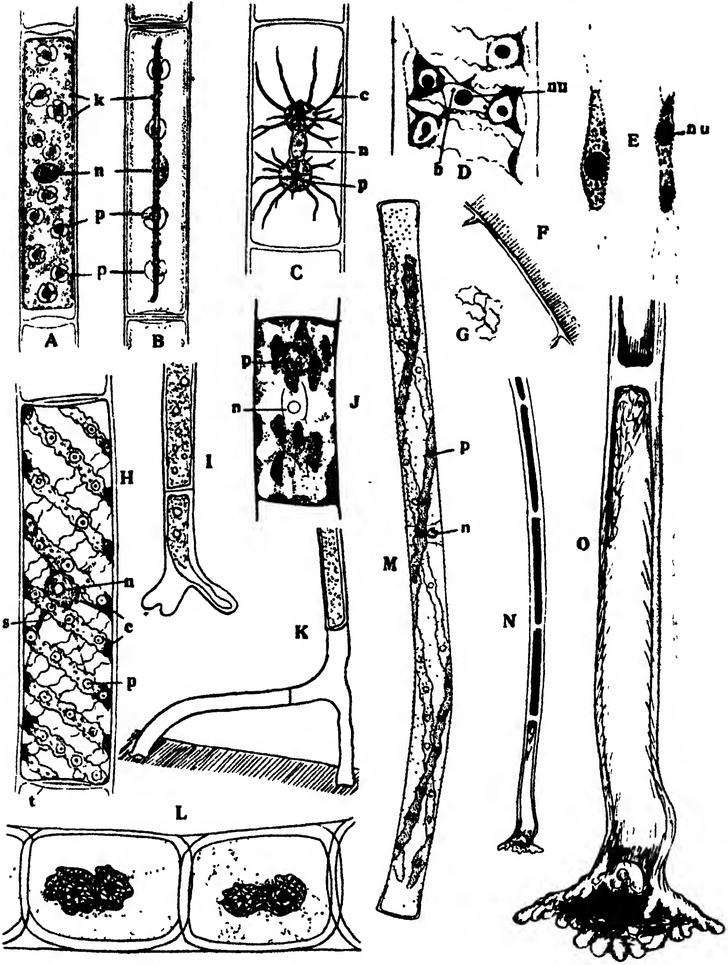

Fig. 98. Vegetative structure of Zygnemoideae. A, B, *Mougeotia scalaris* Hass., surface and profile positions of chloroplast. C, *Zygnema* sp. D, *Spirogyra varians* Kütz., nucleus. E, *S. majuscula* Kütz., nuclei. F, G, *Zygnema* sp., membrane with mucilage, in section (F) and surface-view (G). H, *Spirogyra* sp. I, K, *Mougeotia* sp., rhizoid-formation. J, *Zygnema peliosporum* Wittr. L, *Zygogonium ericetorum* Kütz. M, *Genicularia elegans* West. N, O, *Spirogyra fluviatilis* Hilse var. *africana* Fritsch, base of threads with attaching cells. *b*, body of unknown nature in nucleus; *c*, chloroplast; *k*, caryoids; *n*, nucleus; *nu*, nucleolus; *p*, pyrenoid; *s*, cytoplasmic strand; *t*, septum. (A–C after Palla; F, G after Klebs; H after Fritsch and Salisbury; I, K after drawings of E. J. Salisbury; L after West and Starkey; M after West; N, O after Fritsch; the rest after Czurda.)

The chloroplasts of *Spirogyra* are either narrow with a smooth margin and a regular axile series of pyrenoids or broad with serrated margins and scattered pyrenoids, the two conditions probably representing merely different states dependent on nutritive conditions. In well-nourished cells they may become much dilated with accumulated starch, and under such circumstances may occupy the greater part of the periphery of the protoplast. On the other hand, under conditions of starvation they become much attenuated (23, 42). Similarly, the chloroplasts of *Zygnema* may at times draw in their processes, while those of *Mougeotia* appear merely as a thin strand occupying a small part of the cell. The bands of *Spirogyra* are often provided with an internal ridge (so that they are T-shaped in cross-section), while in other cases they are more gutter-shaped with the concave surface outwards. In rare cases they may be branched ((82), (148) p. 171). The pyrenoids usually project markedly on the inner surface.

Kolkwitz (91) showed that the chloroplasts of *Spirogyra* elongate both by apical and intercalary growth, the latter conditioning the separation of recently divided pyrenoids. According to Czurda ((42) p. 9; cf. also (132)), however, the majority of the pyrenoids in *Spirogyra* and *Mougeotia* arise *de novo* during active cell-division. In *Sirogonium* (fig. 103 B) and a few species of *Spirogyra* the bands run almost longitudinally. The chloroplasts of *Mougeotia* ordinarily present their surface to the light, but on exposure to strong sunlight rotation to the profile position occurs in about thirty minutes (cf. fig. 98 A, B, and (97), (157) p. 26, (160)).

Chloroplasts of a special type are met with in *Zygogonium* (56, 181).[1] Here the cells contain but a single axile chloroplast which is deeply constricted and sometimes twisted at the middle, with one pyrenoid in each of the irregular lobes (fig. 98 L); the chloroplast divides into two just prior to cell-division.

The cell-sap is often rich in tannins and upon this depends the use of species of *Spirogyra* in diverse permeability experiments. In *Zygogonium ericetorum* the sap is coloured violet or purple by phycoporphyrin (95, 114); the purple colour is usually not apparent in shaded situations, but rapidly develops on exposure to stronger light (56). Streaming movements of the cytoplasm are not uncommonly seen in *Spirogyra*. Palla (127) first drew attention to the frequent occurrence in the cells of diverse genera (also among Desmids) of small bodies (caryoids, fig. 98 A, B, *k*), regarded as proteins, whose exact nature and function is not yet ascertained (cf. also (44)).

The single nucleus is always situated in the middle of the cell, being apposed to one side of the chloroplast in *Mougeotia* (fig. 98 A, B, *n*) and *Debarya* and lying between the two chloroplasts in *Zygnema* (fig. 98 C, J, *n*). That of *Spirogyra* (27, 40) is in the narrow forms angular in shape, the corners being in direct contact with the

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[1] Lagerheim's *Pleurodiscus* (95) is probably but a form of this species (cf. (158)).

adjacent pyrenoids (fig. 98 D), while in the broader forms it is lenticular or flatly cylindrical and suspended by cytoplasmic threads within the central vacuole (fig. 98 E). The nuclei of the latter type usually present their edge to the observer. The detailed structure and division of the nucleus of *Spirogyra* have formed the subject of frequent study,[1] and the majority of workers have concluded that the nucleolus contains the bulk of the chromatin. Geitler (64), however, using paracarmine as a stain followed by mounting in Venetian turpentine, showed that at a time when the chromosomes are fully differentiated the nucleolus still persists in an unaltered form (cf. fig. 10 C, p. 70). The nucleus of *Zygnema* (51) appears to have a clear chromatin reticulum.[2]

The spindles seem to be intranuclear (132). According to Conard (27) *Spirogyra majuscula* forms a double spindle, of which only the inner arises from the caryolymph. In *S. mirabilis* Peterschilka (133) describes an amitotic nuclear division. In some species of *Spirogyra* the nuclei contain one or two small stainable bodies (fig. 98 D, *b*) of unknown function, apart from the large nucleolus (35); these bodies disappear at the end of the metaphase, to reappear in the telophase. A few workers have reported centrosomes at the spindle poles in some of the larger species (167, 188).

The cell-wall is composed of a single piece in most Zygnemoideae and is usually moderately thin. The outermost layer is constituted by an often well-defined cuticle which stains yellow with chlor-zinc-iodide, whilst the rest of the wall gives cellulose-reactions. There is generally a more or less conspicuous, external pectose mucilage-sheath to which the members of this group owe their slimy feeling. In some few cases in the living alga, but more usually after treatment with appropriate stains (e.g. methyl violet), a fibrillar structure of the mucous envelope (perpendicular to the surface, fig. 98 F) can be detected ((86) p. 336). Although this suggests an excretion of mucilage through pores in the wall, such pores have not as yet been demonstrated. The minute rods to which the fibrillar appearance is due are arranged in a reticulate manner when viewed from the surface (fig. 98 G). The comparative freedom from epiphytes which is characteristic of the Zygnemoideae is usually ascribed to the presence of the mucilage-envelope, although it has also been suggested that it is due to continuous surface-growth of the membrane which does not admit of a firm hold (21); other factors may, however, come into play (cf. (147)). Epiphytes are not uncommonly found on conjugating threads when, according to Tiffany (169), the transformation of pectose into water-soluble pectin ceases.

The growth of the threads is never in any way localised, any and every cell, apart from the attaching cell when present, being capable

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[1] See (10), (34), (116), (119), (120), (168) p. 171, (174), (191), (192).

[2] It may be doubted whether Merriman's account of division (115) is correct in its details (cf. also (197)).

of enlargement and division. The division of the nucleus is followed immediately by the development of a septum whose mode of formation has been studied especially in *Spirogyra* ((168) pp. 171, 349; cf. also (29)). As the daughter-nuclei are constituted, the fibres of the spindle commence to fuse with one another and at the same time to bulge outwards towards the longitudinal walls, where they meet and fuse with an annular projection of the cytoplasm resulting from a local accumulation in the peripheral layer. Within this cytoplasmic projection, in the neighbourhood of the longitudinal wall, a delicate membrane is suddenly formed, the inner edge of which, covered in by cytoplasm, gradually grows until the cell-cavity is bridged across (fig. 99 A). The chloroplasts are simply cut in two by this septum. In *Zygnema* and *Mougeotia* division of the chloroplasts usually precedes that of the protoplast. The daughter-cells subsequently deposit secondary thickening layers of cellulose which are proper to the individual cells.

By brief exposure to temperatures below the freezing-point or by the addition of small quantities of anaesthetics to the water the division-process takes place abnormally, with the result that cells with two nuclei and others without a nucleus are obtained. A discussion of these matters and of the conclusions drawn from them is, however, beyond the scope of this book (cf. (65), (66), (121), (193), (194)).

FRAGMENTATION OF THE THREADS

In most genera dissociation of the filaments into short lengths or even into separate cells readily occurs, a feature which is specially pronounced in the Gonatozygaceae. The mature transverse walls frequently show a more or less complex structure which is related to this fragmentation and was first studied by Benecke (7). In *Mougeotia* the septa at an early stage split into two circular discs which, according to Lloyd ((100) p. 277), are separated by gelatinous substance. The two parts of the septum frequently bulge apart, so that the latter appears biconvex (figs. 98 A, 99 B), and in this condition, as long as the cells are turgid, the intervening mucilage is compressed. When, however, the turgor of a cell diminishes, the septum becomes bulged into it by the higher pressure in the adjacent cell (fig. 99 C) and the simultaneous dilation of the mucilage increases the curvature. As a result of these happenings a shearing strain is exerted on the common longitudinal wall of the two cells which leads to rupture (cf. fig. 99 C). The same may occur in some species of *Spirogyra*.

In other, relatively narrow species of this genus the middle lamella of the septum develops on either side a cylindrical ring-like ingrowth (resembling a collar) over which the subsequent apposition-layers are deposited (fig. 99 D, F); such septa are described as *replicate* (25). By

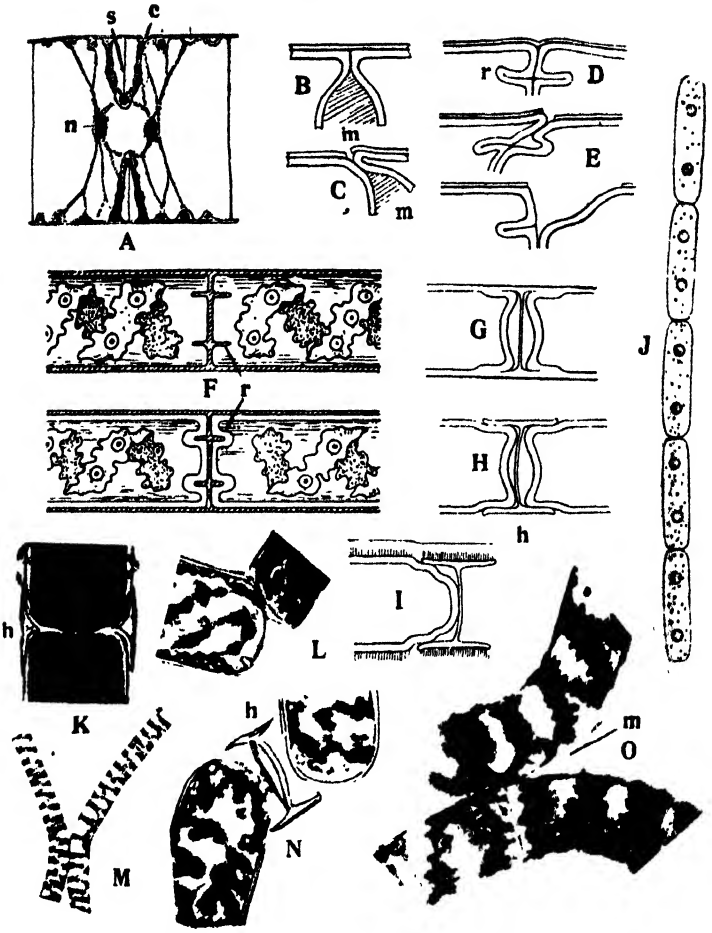

Fig. 99. Cell-division and fragmentation. A, *Spirogyra* sp., cell-division. B, C, *Mougeotia* sp., mechanism of cell-disjunction (diagrammatic). D, E, *Spirogyra Weberi* Kütz., replicate walls, cell-disjunction (diagrams). F, *Spirogyra* sp., stages in development of replicate septa. G–I, *S. colligata* Hodgetts, structure of septum and mode of disjunction, in H the H-piece is clearly recognisable. J, *Debarya desmidioides* West. K, L, N, *Spirogyra nitida* (Dillw.) Link; K, H-structure in septum; L, N, cell-disjunction. M, O, *S. longata* Vauch., adhesion. *c*, chloroplast; *h*, H-piece; *m*, mucilage; *n*, nucleus; *r*, replication of septum; *s*, septum. (A after Strasburger; F after Cohn; G–I after Hodgetts; J after West; the rest after Lloyd.)

the dissolution of the middle lamella the cells are again left connected only by their longitudinal walls. The ingrowth usually becomes evaginated after the cells have broken apart (fig. 99 E), so that the detached cell has a characteristic rounded extremity. Rupture is again no doubt largely due to alteration in the turgor of a cell leading to the development of shearing strains. Species of *Spirogyra* with replicate end-walls usually fragment more readily than those with plane septa, but the exact purpose of the replication is scarcely yet clear.

A different method of cell-disjunction occurs in some of the larger, more thick-walled species of *Spirogyra*, such as *S. nitida*; this method was first described by Strasburger ((167a) p. 57) in *S. orthospira.* According to Lloyd ((100) p. 279) the walls in such cases consist near the septa of short H-pieces (cf. also (165), (202)) which are specially obvious in *S. colligata* Hodgetts (75) (fig. 99 H), but stand out distinctly also in other species after treatment with sulphuric acid or zinc chloride (fig. 99 K). It is, however, at present not clear whether the H-structure is normally present in the wall or whether it arises only in relation to disjunction. The process of disjunction commences with local hydrolysis of the longitudinal walls along a circular transverse line coinciding with the ends of an H-piece (fig. 99 H, K). The process of solution first leads to a disappearance of the mucilage-layer and then gradually extends into the wall, until the innermost layer investing the protoplast is reached, after which it spreads round the end of the cell, thus setting free the innermost layer from the middle lamella of the septum. As the layer around the protoplast becomes free it is distended by the turgor of the cell and ultimately the end rounds off, causing it to slip from the H-piece (fig. 99 I, N). The free end often has an exceedingly thin cellulose-membrane devoid of mucilage, but this very soon appears. The H-pieces described by Steinecke (163, 165) in *Zygogonium ericetorum* are probably merely formed by the rupture of the outer layers of the membrane of germinating thick-walled akinetes, a condition comparable to that seen in *Binuclearia* for instance (p. 206).

In *Debarya desmidioides* (184), where there are constrictions between the cells of the filaments (fig. 99 J), the latter dissociate with great ease into the individual cells, conjugation always occurring in this condition. Much the same is the case in *Gonatozygon* and *Genicularia.*

THE PROCESS OF CONJUGATION

Most Zygnemoideae conjugate readily, the process occurring more frequently in low-lying areas than in upland districts. In north temperate regions it ensues mainly between February and June (31, 59). As in so many other cases nitrogen-deficiency appears to be an important conditioning factor (8). Czurda (201), however, finds that conjugation does not take place until the climax of vegetative activity is passed (cf. p. 49), when an increase in the *p*H conditions its occurrence. Conjugation usually occurs between two filaments which become ranged parallel to one another, although cases in which from three to six or more are involved are occasionally observed ((16), (30), (184) p. 42). The juxtaposition of the threads is brought about by slow movements which have been specially studied in *Spirogyra* (77), although the mechanism is scarcely clear.

Oltmanns ((125) p. 96) suggests that the movement is related to the secretion of mucilage and that it probably occurs only in contact with a firm substratum. Langer (96) finds that isolated threads exhibit no change of position, which is only observed when the filaments are crowded. Movement is not limited to the period of conjugation, but occurs also during active vegetative growth. At such times the movements have been regarded as resulting from differences in rate of growth, but Langer could find no evidence for this. According to him the movements are more rapid in darkness; their direction is not determined by light, although gravitational stimuli seem to come into play.

(*a*) ZYGNEMACEAE

The process of conjugation has been studied by many different observers, but it is only within the last decade that the true course of events has been established (37, 40, 73, 89, 99, 101, 102, 146, 148).[1] At present a detailed study has been undertaken only of the genus *Spirogyra*, but it cannot be doubted that other Zygnemoideae will fall more or less into line. It is recently divided cells that conjugate ((37) p. 450, (101) p. 76), such cells being therefore commonly shorter than the vegetative ones. At the commencement of conjugation the threads become intimately glued together by mucilage (fig. 100 A).

Such agglutination may, however, also occur without conjugation. Pairs of threads of both *Spirogyra* and *Mougeotia* commonly exhibit local adhesions and at these points there are usually prominent knee-shaped bendings or geniculations in the threads (fig. 99 M, O). According to recent workers (37, 101, 102) such adhesions are due to a thin disc-like pad of mucilaginous material (fig. 99 O, *m*), often readily visible in *Mougeotia*, though generally difficult of recognition in *Spirogyra*. This is formed by an alteration of the outer superficial zone of the cell-wall, although it is possible that in some cases only the mucilage-sheath may be involved ((146) p. 239). No doubt the juxtaposition and agglutination of the threads at the commencement of normal conjugation takes place in the same way. The adhesions are believed to result from a contact stimulus. There can be little doubt that they represent initial stages in conjugation in which the further steps are not realised, since in *Mougeotia* conjugation tubes may be developed to a varying extent at the points of adhesion; adhesions have also been observed between threads of *Spirogyra longata* exhibiting lateral conjugation.

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[1] For the older literature, see (6), (19), (69), (87), (117), (126), (172), (184). Some of De Bary's figures (6) are correct in many details.

After juxtaposition of the threads the next step in conjugation is the putting out of papillae from one of each pair of opposite cells (fig. 100 B, D). According to Saunders (146) these first formed papillae usually all arise on one filament of a pair (cf. fig. 100 D–G), but this may be either the male or the female filament; in some few cases the first papillae appear indifferently on the cells of either thread. Subsequently, papillae usually arise from opposite and corresponding points on the other filament, so that the two papillae are in contact from the first moment of their formation and, as they elongate to form the conjugation processes (fig. 100 C), the two threads gradually become pushed apart. The first to recognise this fact was Chodat (20) in discussing the conjugation of a *Mougeotia* (cf. also (20 a) p. 45).

According to Lloyd ((102) p. 49) the ends of the processes are composed of the inner parts of the wall only, the outer layers becoming softened and pushed aside. The conjugation process produced by the female cell is usually thicker and shorter than that formed by the male (cf. fig. 100 C), and in some species only the male cell develops a process which forms the entire conjugation canal ((40) p. 255, (89) p. 29). The processes have been compared to the rhizoids commonly formed in Zygnemoideae, both of which probably result from a contact stimulus ((20), (37) p. 455, (162)). Kniep ((89) p. 30) and others, however, believe that the development of the conjugation-processes is essentially due to a chemical stimulus. Especially in species of *Zygnema*, where the threads often have a well-developed mucilage-sheath, the actual cells may remain rather widely separated after approximation so that the papillae do not arise in contact, but grow towards each other through the intervening mucilage (fig. 101 B) after the manner formerly assumed to represent the normal method of conjugation in Zygnemaceae.

As soon as conjugation sets in the cells of the two threads accumulate abundant starch (cf. also (76 a), (200)), although this subsequently disappears again from those not involved in conjugation; according to Lloyd (99) mucilage-globules also appear. During the early stages of conjugation the osmotic pressure of the sap sinks considerably (87), more in the male than in the female cells, which is presumably due to a decrease in osmotically active substances, possibly to the conversion of sugars into starch. The permeability is lowered and, as Weber (177) first showed, there is an increase in the viscosity of the protoplast, although according to Lloyd ((99) p. 131, (101) p. 82) this is not uniform, but is greatest at the posterior end of the male and least in the region of fusion. At the same time nucleus and nucleolus decrease in size. When the processes have reached their full length, their end-walls are dissolved, so that an open, usually relatively narrow conjugation tube is formed (fig. 100 F, H). The prolongations

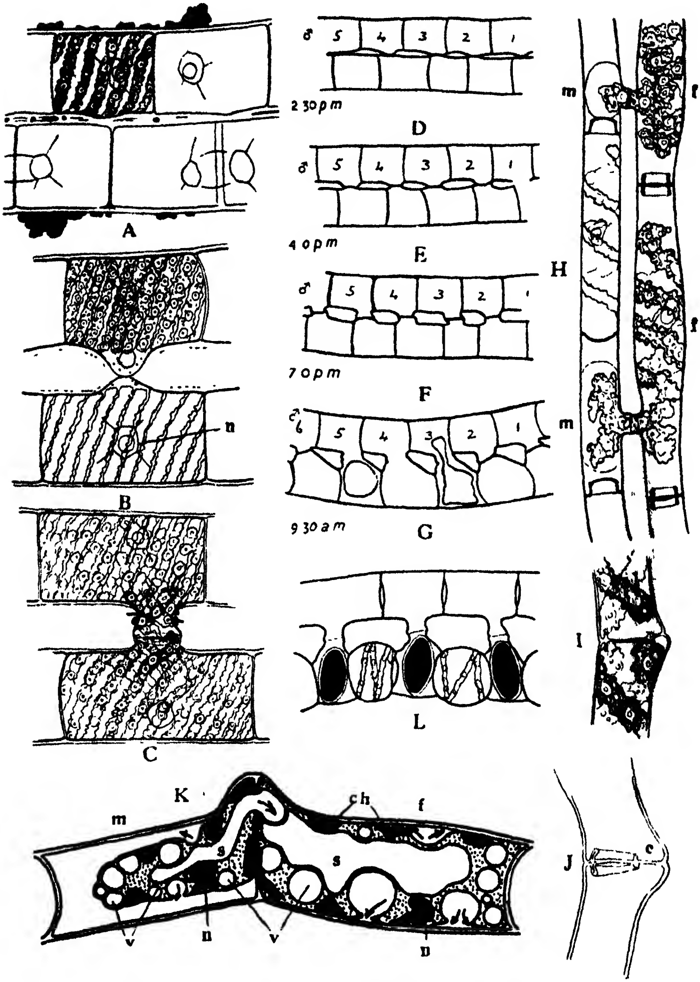

Fig. 100. Conjugation in *Spirogyra*. A–C, *S. setiformis* (Roth) Kütz., successive stages in scalariform conjugation. D–G, *S. varians* (Hass.) Kütz. var. *scrobiculata* Stockm., the same. H, *S. Weberi* Kütz., sexual fusion. I, J, *S. Hassallii* (Jenn.) Petit, formation of canal in lateral conjugation. K, *S. longata* Vauch., sexual fusion, lateral conjugation. L, *S. varians*, completed conjugation. *c*, canal; *ch*, chloroplast; *f*, female and *m*, male gametes; *n*, nucleus; *s*, central vacuole; *v*, contractile vacuoles. (D–G after Saunders; K after Lloyd; the rest after Czurda.)

of the two protoplasts that have extended into the processes are thus brought into direct touch.

When the open canal is established the male protoplast, without losing contact with the female, contracts away from its wall and the process of fusion commences (fig. 100 H), surface tension probably gradually pressing the male through the conjugation tube into the female protoplast.[1] It is not until the male has passed entirely over into the female that the latter in its turn contracts away from its membrane (cf. (126)). According to Lloyd the contraction of the gametes is due to the discharge of liquid from a number of large, nearly spherical contractile vacuoles (cf. also (19)) which may be sufficiently numerous to produce a frothy appearance and arise sooner in the male than in the female (cf. fig. 100 K, *v*, showing lateral conjugation). These vacuoles are stated to receive water, probably containing some solutes ((102) p. 54), by diffusion from the central vacuole and to discharge it into the space between the protoplast and the cell-wall. In the male protoplast they appear at the posterior and spread to the anterior end (fig. 100 K), while in the female the order of appearance is in the opposite direction. Similar vacuoles are also operative in bringing about the final contraction of the zygote.

According to Lloyd ((101) p. 90; cf. also (89) p. 24) this course of events does not obtain in all species of *Spirogyra*. In *S. maxima* and probably in other large species considerable contraction of the male, and sometimes also of the female gamete, may take place before fusion. The male gamete, however, remains in connection with the tip of the male conjugation process or with some part of the tube. In the premature contraction these species behave more after the manner assumed in the older accounts of the conjugation-process. In many cases the female cells become much swollen after fusion of the gametes.

The ladder-like or scalariform method of conjugation described above is that habitual in *Spirogyra*, but another method (*lateral conjugation*) is occasionally observed and in some species (e.g. *S. affinis*, *S. tenuissima*) may even be the rule. In this case there is no sexual differentiation between the filaments, and the conjugation-processes arise from adjacent ends of neighbouring cells. They are formed by a gradual protrusion of the longitudinal wall on either side of the septum (fig. 100 I, J), the adjacent portion of which becomes stretched in the same measure ((99) p. 130, (37) p. 472). This can be regarded as a production of two processes which, however, as in scalariform conjugation, are in contact from the first. The septum in the region of the protrusion then breaks down (fig. 100 K), although in *S. longata* according to Lloyd but a minute pore is at first formed.

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[1] In *Zygnema* according to Dangeard (43) the male gamete twists through a right angle before fusion.

The further events leading to fusion are the same as in scalariform conjugation (cf. fig. 100 K). The same filament may sometimes show both scalariform and lateral conjugation.

In *Spirogyra* the male gamete always passes over into the female and the zygospore is lodged in the female cell (fig. 100 L). In scalariform conjugation all the cells of a filament usually behave alike and all the zygotes are situated in the female thread; cross-conjugation in which some cells of the filaments act as males and others as females, so that perfectly normal zygospores are formed in both threads, is exceedingly rare ((32), (33), (36), (184) p. 47). Relative sexuality, in which one thread behaves respectively as male and female to two others, is also on record ((89) p. 39). In lateral conjugation a cell harbouring a zygospore is always adjoined by an empty cell.

In some species with replicate walls showing lateral conjugation (e.g. *S. Spreeiana* Rabenh.) male and female cells always occur in pairs, which are separated by a plane wall; after conjugation, therefore, one finds pairs of cells with zygotes separated by pairs of empty cells ((89) p. 35, (172)). Tröndle regards such pairs of male or female cells as sisters whose sex is determined before the division to form the pair takes place. This state of affairs does not, however, obtain in the majority of species showing lateral conjugation.

Species in which only scalariform conjugation occurs are no doubt in part dioecious with genotypic sex-determination. Czurda (38, 39) has, however, shown that in clones resulting from isolated non-conjugating cells, separated from sexually reproducing threads, abundant conjugation may in many cases be observed, indicating that the sex is here determined phenotypically.

Certain species of *Zygnema* (e.g. *Z. stellinum*, fig. 101 F) exhibit a process of conjugation just like that of *Spirogyra*, and it is justifiable in such cases to speak of physiological anisogamy, although the gametes are not morphologically distinct. In *Z. stellinum* Steinecke (166) has recorded sexual dimorphism, the female cells being longer and broader and having larger chloroplasts and pyrenoids than the male. Not all Zygnemaceae, however, display the anisogamy just described. Several species of *Zygnema* (e.g. *Z. pectinatum*, fig. 101 A) and all those of *Debarya* (fig. 101 D, H) exhibit union of the gametes and formation of zygospores within the conjugation-canal, so that conjugation is both morphologically and physiologically isogamous. In some species of *Debarya* (171) and *Zygnema* the empty conjugating cells become filled with deposits of cellulose which are laid down in successive strata as the protoplasts recede during fusion (fig. 101 C, I).

The fact that the process may be isogamous or anisogamous in the same genus (*Zygnema*) leads one to suspect that sexual differentiation may not be very pronounced, the more as lateral and scalariform

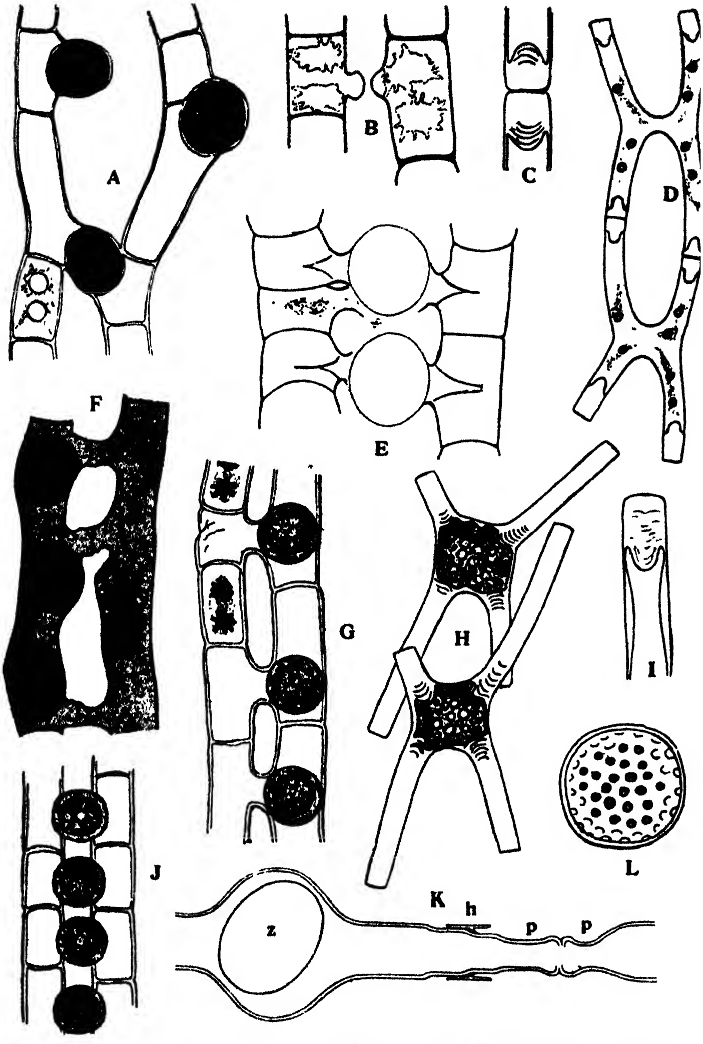

Fig. 101. Conjugation in Zygnemoideae. A, *Zygnema pectinatum* (Vauch.) Ag. (after Fritsch), lateral and scalariform conjugation in the same filament. B, E, *Z. circumcarinatum* Czurda (after Czurda); B, commencing papilla-formation; E, late stage. C, D, H, I, *Debarya Hardyi* West (after West); D, early conjugation-stage; H, zygospores; C, I, extremities of emptying gametangia to show thickening. F, L, *Zygnema stellinum* (Vauch.) Ag. (F after West; L after Boergesen); F, completed conjugation; L, zygospore. G, J. *Z. peliosporum* Wittr. (after Fritsch & Rich); G, anisogamous and J, isogamous conjugation. K, *Spirogyra colligata* Hodg. (after Hodgetts). *h*, H-piece; *p*, conjugation-process; *z*, zygospore.

conjugation have not uncommonly been observed in the same filament (cf. fig. 101 A). In the case of *Z. peliosporum* (60) material from the same habitat, though collected in different years, has been found on one occasion to show the spores formed in the one conjugating cell, on the other in the conjugation tube (cf. fig. 101 G, J), and despite Czurda's criticism (39) I am still of the opinion that in this case we have an instance in which the degree of sexual differentiation is variable.

In the genera, whose conjugation has so far been discussed (Zygnemaceae), various exceptional occurrences have come to light. Thus, Czurda (39) has described a form (*Zygnema circumcarinatum*) in which the processes break down at their apices before they meet, the protoplasts gradually escaping from the open ends and fusing to form a zygote between the two papillae (fig. 101 E). Similar features are seen in the conjugation of some Desmids. Hodgetts' *Spirogyra colligata* (75) is remarkable in that lateral conjugation in some cases takes place by the protrusion of papillae from the two parts of the septum, the conjugating cells being pushed apart by their elongation, although remaining connected by the papillae (fig. 101 K).

(*b*) MOUGEOTIACEAE

In other genera of Zygnemoideae, which can be grouped as Mougeotiaceae, various specialisations in the conjugation process are apparent. In *Mougeotia*[1] the gametes are produced from only a part (including nucleus and chloroplast) of the protoplast of the gametangium.[2] The conjugation-canal may be formed either by means of papillae as in the Zygnemaceae, or merely by the approximation and subsequent fusion along the point of contact of geniculate pairs of cells. After fusion the zygote does not immediately secrete a membrane of its own, but becomes separated from the surrounding sterile parts containing the unused cytoplasm by variously orientated walls. Of these sterile cells there may be two, three, or four, the number depending upon the position and size of the zygospore and being subject to some variation in one and the same species (fig. 102 A–D). It is peculiar to *Mougeotia* that these remains of the gametangia persist around the mature zygospore, the outer part of whose envelope is thus formed by the conjugation-canal and the above-mentioned septa, whilst further thickening layers are gradually secreted internally by the zygote (fig. 102 B, C).

[1] It is not uncommon to find threads of this genus in contact by means of conjugation-papillae without a completion of the process being attained. Geitler (63) suggests that these are cases of apomixis.

[2] This may also happen occasionally in *Spirogyra* and *Zygnema* (cf. (22)). In *Mougeotia* the residual cytoplasm is that of the plasma-membrane (6).

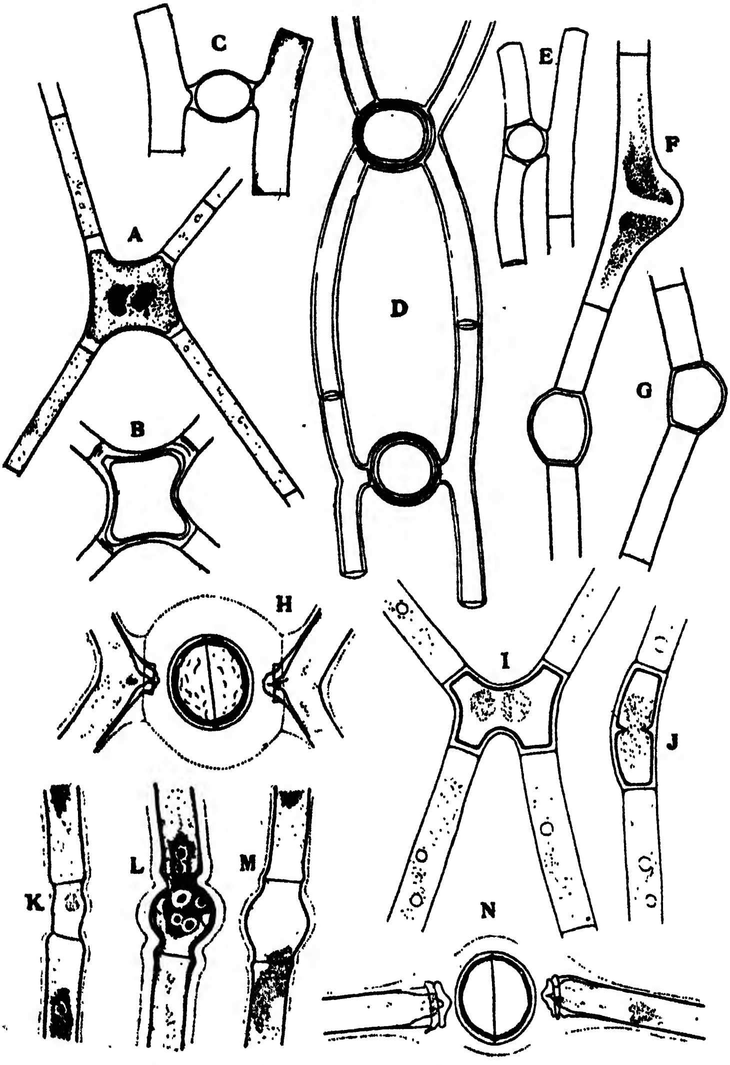

Fig. 102. A, *Mougeotia* sp. B, *M. capucina* (Bory) Ag., zygospore. C, *M. scalaris* Hass., zygospore. D, *M. calcarea* Wittr. E, *M. tenuis* (Cleve) Wittr. F, G, *Gonatonema ventricosum* Wittr. H, K–N, *Mougeotia oedogonioides* Czurda; H, scalariform conjugation; K–N, different stages in lateral conjugation. I, J, *Temnogametum heterosporum* West; I, scalariform and J, lateral conjugation. (B, C, E after Transeau; D after Wittrock; F, G, I, J after West; the rest after Czurda.)

The bulk of the species of *Mougeotia* are isogamous, but the zygospores are often situated nearer to one of the conjugating cells, whose conjugation-process is thicker and shorter than that of the other. In *M. tenuis* (24), in fact, the zygote is located mainly in one of the two conjugating cells (fig. 102 E). *M. oedogonioides* Czurda (41)[1] shows a complete gelatinisation of the central inflated part of the conjugation-canal after fusion of the gametes, while at the same time the basal parts of the original papillae close at their free ends, the zygote surrounded by a wide mucilage-envelope lying suspended between the two (fig. 102 H). Lateral conjugation in this species is accomplished in essentially the same manner as in *Spirogyra colligata* (fig. 102 K–N).

In the little known *Temnogametum* (171 *a*, 183) the gametes are cut off, already prior to fusion, as specially short cells brought into contact by geniculation and fusing without any contraction of the contents, so that the zygote fills the whole of the two cells (fig. 102 I). Lateral conjugation of similar short cells is accomplished merely by solution of the intervening septum (fig. 102 J). The special features appear only as a modification of what normally occurs in *Mougeotia*, the separation of the gametes taking place before, instead of after, fusion, and there may be some justification for including the genus as a section of *Mougeotia* ([illegible]).

In *Zygogonium ericetorum* (6, 74) the gametes are again produced only from part of the cytoplasm of the gametangia. Before the canal is fully established, the greater part of each protoplast passes into the process and becomes cut off by a curved wall (fig. 103 C, *a*). Within the cell thus formed the protoplast secretes an independent thin membrane and, after the fusion of the gametes which commences by the formation of a pore (fig. 103 D, lower part) that gradually enlarges (fig. 103 D, upper part), these membranes unite to form the outermost layer of the zygote-wall (fig. 103 E).[2]

Morphological anisogamy is found only in *Sirogonium* (*Choaspis*) (6), where the conjugating cells meet by geniculation, especially of the female cell, and no processes are formed; at the point of contact there is a conspicuous ring of mucilage (fig. 103 B, F, *r*), probably representing the edge of the adhesive pad (cf. p. 323). As a general rule the conjugating cells are cut off by preparatory divisions, whereby gametangia of different sizes are produced (fig. 103 B). In the male (*m*) a first division separates off a small sterile cell (*s*) at one end, after which a second much larger cell (*s'*) is cut off at the other end; in the

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[1] A closely related form showing similar features in the conjugation-process is Iyengar's *M. adnata* (80).

[2] I can fully confirm De Bary's and Hodgetts' accounts of the conjugation-process which has been observed several times in fresh material during wet winter weather. Czurda's ((41) p. 279) refusal to accept this form, owing to the fact that zygotes with a mature membrane have not been observed, is scarcely relevant. The conjugation-canal itself is so thick and gelatinous that an additional envelope is hardly necessary.

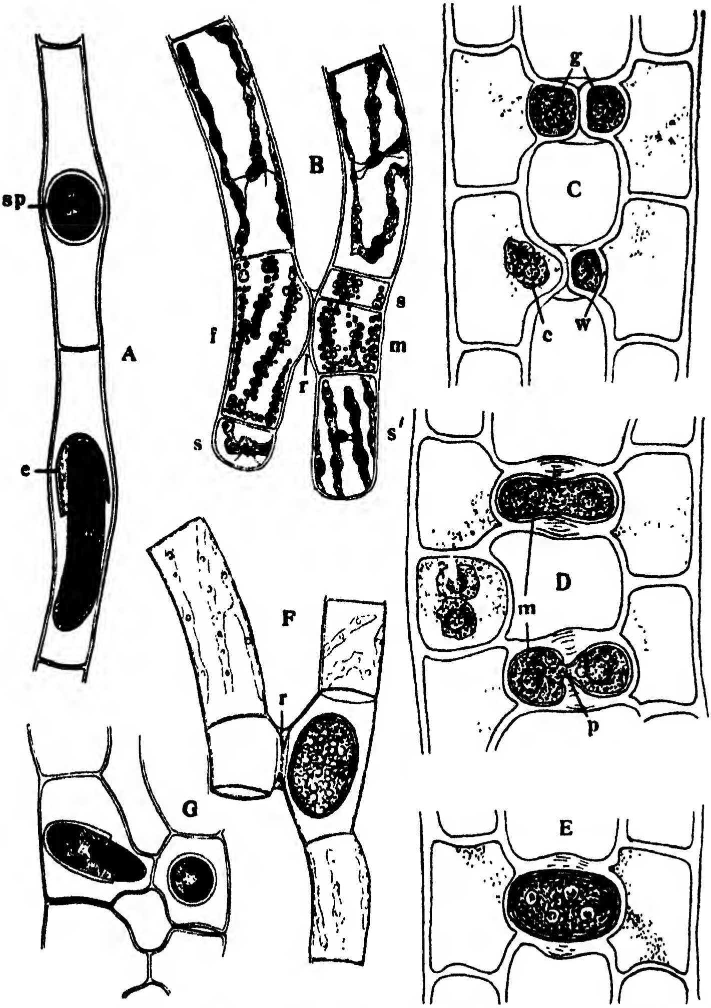

Fig. 103. A, *Spirogyra mirabilis* (Hass.) Kütz., parthenospores, the lower one germinating. B, F, *Sirogonium sticticum* Kütz.; B, early and F, late stages in conjugation. C–E, *Zygogonium ericetorum* Kütz., successive stages in conjugation; E, zygospore. G, *Spirogyra varians* (Hass.) Kütz., parthenospores, the one on the left germinating. *c*, chloroplast; *e*, envelope of spore; *f*, female gamete; *g*, gametes; *m*, male gamete; *p*, conjugation-process; *r*, mucilage-ring; *s*, *s'*, sterile cells; *sp*, parthenospore; *w*, septum cutting off gametangium. (A, G after Klebs; B, F after De Bary; the rest after Hodgetts.)

female cell (*f*) of the opposite filament there is only one division separating off a small sterile cell (*s*), so that the resulting female gametangium is much larger than the male. The zygospore is formed in the female cell (fig. 103 F). Lewis (98) has described a species of *Spirogyra*, under the generic name *Temnogyra*, in which a large sterile cell with scanty contents is cut off in either thread before the gametangium which contains most of the chloroplast is differentiated. This serves to link *Spirogyra* with *Sirogonium* which Printz (139) and others regard but as a section of the former genus. Whatever views one may hold as to this, there is no doubt about the inequality of the conjugating cells in *Sirogonium* and that this usually arises prior to conjugation by unequal division.

GERMINATION OF THE ZYGOSPORES

The ripe zygospores of the Zygnemoideae are usually spherical or ellipsoidal and possess a thick wall which is composed mainly of cellulose and is commonly three-layered, the outer layer being cuticularised and the middle one often exhibiting distinctive markings (cf. fig. 101 L). According to Conard (26) this layer is composed of two halves in *Spirogyra majuscula*. The contents of the zygote accumulate a large amount of fat which arises by conversion of the starch and is often coloured red. In the isogamous *Zygnema* the contracted chloroplasts of the two gametes remain recognisable in the zygospore up to late stages, while in the anisogamous forms and in *Spirogyra* those of the male usually disintegrate at an early stage ((18), (94), (172); cf. however (159)), in *Temnogyra* before the male protoplast passes over into the female.

Nuclear fusion appears to be delayed for some little time after the amalgamation of the gametes. Division of the fusion nucleus may either take place soon after, during the ripening of the zygospore ((173) pp. 610, 611) or only just before germination, as in other Conjugales. Of the customary two nuclear divisions (fig. 104 A, B) the first generally accomplishes reduction (81, 94, 173), but some species of *Spirogyra* are stated to be peculiar in the fact that the second is the reduction division ((173) p. 609). One of the four nuclei formed enlarges (fig. 104 C, D), while the others gradually abort, a single individual (fig. 104 E, G) thus resulting from each zygote (cf. also (138)). As a preliminary to germination the abundant fat is converted to starch, whilst the chloroplasts become more distinct. Thereupon the outer thick layers of the zygospore-membrane are burst at one end and the contents, surrounded by the innermost layer, grow out as a long tube (fig. 104 E, G, H) which soon undergoes division into two cells. The lower of these contains scanty chlorophyll and often appears colourless for the greater part of its length, and in *Spirogyra* and *Mougeotia* (198) it may develop into a definite rhizoid which often remains in the zygospore-membrane for some time (fig. 104 H); the upper proceeds to divide to form the thread. In *Zygnema* the distinction into base and apex is scarcely evident.

In one species of *Zygnema* (*Z. reticulatum* Hallas) the azygospores

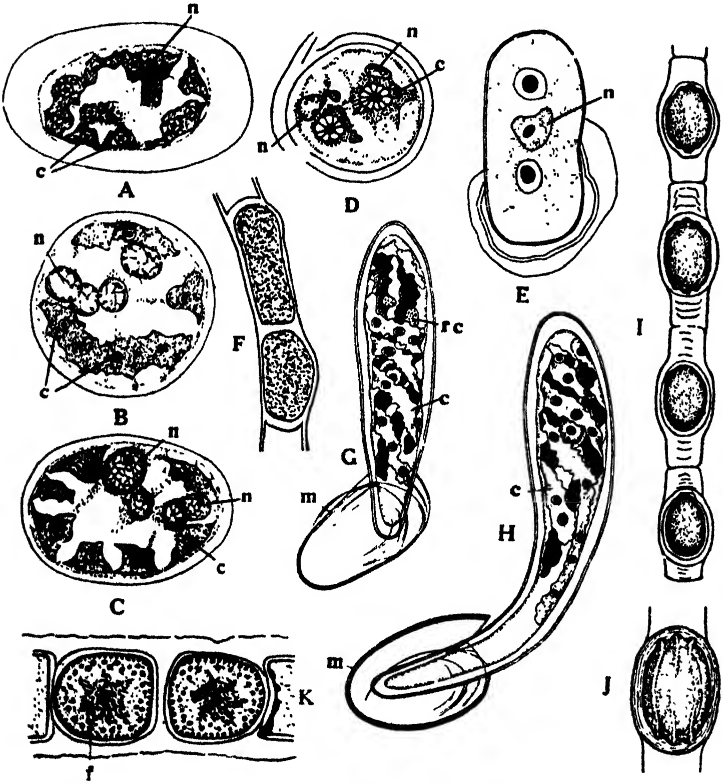

Fig. 104. A, *Spirogyra calospora* Cleve, second nuclear division in zygote. B, C, *S. longata* Vauch.; B, quadrinucleate stage; C, degeneration of three nuclei. D, E, *Zygnema stellinum* (Vauch.) Ag.; D, degeneration of three nuclei; E, development of young plant. F, *Mougeotia capucina* (Bory) Ag., akinetes. G, H, *Spirogyra neglecta* (Hass.) Kütz., successive stages in germination. I, J, *Zygnema fertile* Fritsch & Rich, azygospores. K, *Zygogonium ericetorum* Kütz., akinetes. *c*, chloroplast; *f*, fat; *m*, envelope of zygospore; *n*, nucleus; *rc*, disintegrating chloroplast. (D, E after Kurssanow; F after Borge; I, J after Fritsch & Rich; K after Fritsch; the rest after Tröndle.)

cf. below) have been observed to give rise to one, two, or three new individuals in germination (70);[1] to base a separate genus on this, as Rosenvinge (145) suggests, is in the present state of our knowledge not warranted. According to Conard (28) the gametes of *Spirogyra majuscula* are only connected by a cytoplasmic bridge in the zygote, and it is within this bridge that nuclear fusion occurs; in germination the two gametes are stated to separate again. This requires confirmation.

Numerous irregularities in the process of conjugation are on record,[2] but these cannot occupy us here. In several Zygnemoideae parthenogenesis occurs as an occasional phenomenon ((89) p. 42). The plainest case is constituted by *Spirogyra groenlandica* (144) in which, after the conjugation-processes have been produced, but usually before the establishment of an open tube, the contents of the gametangia round off and, secreting a membrane, develop into parthenospores (*azygospores*). Czurda ((42) p. 146) expresses doubts whether the phenomena described by Rosenvinge represent a normal condition, although much the same obtains in species of *Mougeotia* and *Zygogonium*. In a species of the latter Iyengar (80) describes formation of azygospores in a manner quite comparable to the normal conjugation-process for this genus.

Klebs (87) was able to bring about the formation of parthenospores artificially in *Spirogyra varians*, a species which usually exhibits normal conjugation,[3] by placing conjugating filaments in a strong solution of sugar (fig. 103 G). In *S. mirabilis* (Hass.) Kütz. (87, 133, 134) there is no indication even of the preliminaries of the conjugation-process, although Czurda (39) obtained such in cultures; the parthenospores are simply formed by marked contraction and rounding off of the contents of the cells (fig. 103 A). *Zygnema spontaneum* Nordstedt (124, 183) at times behaves similarly, but at others exhibits normal conjugation (cf. also (52)). Lewis also records parthenogenesis in *Temnogyra*.

Formation of parthenospores is also a normal phenomenon in *Gonatonema* ((89) p. 64, (199)), usually regarded merely as a section of *Mougeotia* with which it agrees in vegetative structure. In this case the protoplast contracts into the middle portion of the cell (fig. 102 F) which becomes somewhat enlarged and is cut off by septa from the empty parts (fig. 102 G); the spore then develops a special wall of its own. Not uncommonly the cells concerned exhibit geniculation, similar to that often shown by conjugating threads of *Mougeotia*. During the development of the spores and just before the rounding off of the protoplast, the latter in rare cases is stated to divide partially

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[1] Cf. also (94) p. 74.

[2] See (19), (20), (61), (65), (113), (150), (184).

[3] According to Czurda ((40) p. 268) parthenospores are also commonly formed in nature by this species.

or completely into two (cf. fig. 102 F). Czurda ((40) p. 282) suggests that these parthenospores may in part at least result from a process of lateral conjugation in which the septum between the fusing cells has broken down (cf. *Temnogametum*, p. 331), but at present there is no evidence for this. Some species of *Zygnema* (fig. 104 I, J) form very characteristic parthenospores (60).

Structures which are probably best regarded as akinetes are formed in some species of *Mougeotia* and especially commonly in *Zygnema*. In the former genus akinete-formation is especially found in the species that inhabit mountain tarns and lakes with a relatively low temperature; in such habitats conjugation is rare and hibernation appears usually to be effected by means of akinetes. In shape the latter mostly differ but little from the vegetative cells, but the walls become markedly thickened, whilst starch and fat accumulate within the protoplast (fig. 104 F). Not uncommonly threads producing such akinetes are encased in a conspicuous and often stratified mucilage-envelope, even when this is not visible around the purely vegetative threads. Puymaly (142) describes specialised akinetes formed from terminal or intercalary cells of the filaments of *Spirogyra fluviatilis*, the cells in question becoming swollen and accumulating much starch. Akinetes are also readily formed in the terrestrial *Zygogonium ericetorum* and in very dry habitats the threads of this species may exist permanently in the akinete-condition (56); the cells here harbour numerous small fat-bodies, frequently arranged in a dense peripheral layer beneath the wall (fig. 104 K, *f*).

Since threads of diverse species of Zygnemoideae often occur intermingled with one another, fusion between filaments of different species is not altogether rare. Cases of this kind have been observed both in *Spirogyra* and *Mougeotia* ((2), (11), (184) p. 43), but no detailed investigations on this subject have so far been carried out. Transeau (170) states in the cases observed by him that the form of the zygospore is determined solely by the female gamete. He believes that segregation in the reduction division results in the production of a number of different types (cf. with the hybrids in *Chlamydomonas* discussed on p. 120). An experimental investigation should sooner or later be possible.

THE CLASSIFICATION OF THE ZYGNEMOIDEAE

Very diverse opinions have been held as to the classification of the Zygnemoideae. West (179) advocated a classification depending on the characters of the chloroplast and Czurda has recently (42) carried this to its logical conclusion by recognising only three genera, *Spirogyra*, *Zygnema* and *Mougeotia*.[1] I am of the opinion, however, that the separation of the zygote by special septa in *Mougeotia* marks a con-

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[1] For other opinions on generic demarcation, see (139), (171).

siderable advance on those vegetatively similar forms in which this does not occur and for which I would maintain the old genus *Debarya*. The latter, as well as *Zygnema* and *Spirogyra*, are regarded as representing the less specialised members of the group. The divisions taking place in *Sirogonium*, *Temnogametum*, and *Zygogonium* prior to conjugation are deemed to be comparable to those occurring in *Mougeotia* subsequent to conjugation. The two families thus distinguished are the Zygnemaceae and Mougeotiaceae (180). The third family, Gonatozygaceae, includes only *Gonatozygon* and *Genicularia* which are regarded as reduced Zygnemoideae in conformity with Oltmanns' views (125); like other members of the suborder they produce a single embryo from the zygote.

Suborder II. *DESMIDIOIDEAE* (PLACODERM DESMIDS)

The true Desmids are remarkable for the diversity of form, the often extraordinary complexity of the cell-outlines, and the marked symmetry. They include some of the most beautiful of microscopic objects. The majority live as single individuals, but a certain number are colonial, the cells being united in most cases to form long filaments (fig. 105 J) which are often twisted. Desmids are essentially free-floating and frequently occur in great abundance in small ponds, in the quiet margins of rocky lakes, in *Sphagnum*-bogs, and in other localities where the water is not alkaline. With the exception of *Cosmarium salinum* Hansg. (71), recorded from brackish waters, they are altogether restricted to fresh waters.

Except in *Closterium* (fig. 105 G) and some species of *Penium* the desmid-cell exhibits a more or less distinct constriction into two perfectly symmetrical halves (cf. fig. 105 A, D, E); each half is termed a *semicell* (*c*) (even where no constriction exists), and the narrower part connecting the two semicells is known as the *isthmus* (*i*). The excavation resulting on either side from the constriction or narrowing of the cell is spoken of as the *sinus* (*si*), and in most deeply constricted forms this is linear (fig. 105 D, E).

There are several thousand known species of Desmids, most of which can be identified by the characteristic features of the vegetative cells. Some are cylindrical with rounded (e.g. *Penium*, fig. 106 H, I), truncate (e.g. *Pleurotaenium*, fig. 105 K), or attenuated (e.g. *Closterium*, fig. 105 G) apices. Many of them are flattened, as is the case with most species of *Cosmarium* (figs. 105 E; 106 A) and all species of *Euastrum* (fig. 105 B, C), whilst in *Micrasterias* (fig. 105 A) the majority of the species are disciform. In such flattened Desmids there are three principal planes of symmetry at right angles to one another and they require to be examined in three positions. The most important aspect is the *front-view* (figs. 105 E; 106 A, *f*) in which the cell is observed in the plane containing the two longest axes and in which it naturally rests. The other important aspects are the vertical or *end-view* (*e*) and the lateral or *side-view* (*s*). In the genus *Staurastrum* the cells have a radiate character, with two-, three-, four-, or more-angled end-views (fig. 105 F), the corners often being drawn out into long processes (fig. 106 F, G). Many of the simpler species of *Staurastrum* have triangular end-views (fig. 105 F).

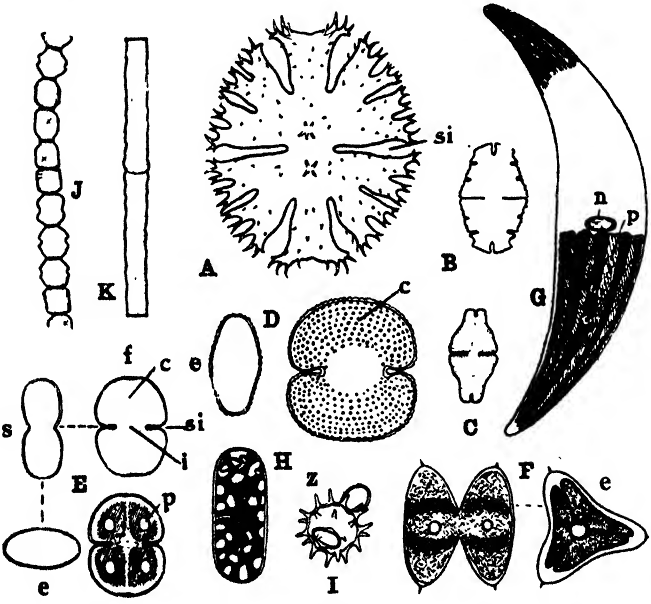

Fig. 105. Common types of Desmids (from Fritsch and Salisbury). A, *Micrasterias*. B, C, *Euastrum*. D, E, *Cosmarium*. F, *Staurastrum*. G, *Closterium*. H, *Cylindrocystis*. I, *Cosmarium Meneghinii* Bréb., zygospore (after West). J, *Desmidium*. K, *Pleurotaenium*. *c*, semicell; *e*, end- and *f*, front-views; *i*, isthmus; *n*, nucleus; *p*, pyrenoid; *s*, side-view; *si*, sinus; *z*, zygospore.

STRUCTURE OF THE CELL

The wall of the desmid-cell (72, 107) invariably consists of two halves, one of these belonging to an older generation than the other. The two halves have bevelled edges and fit so closely over one another and are so firmly connected that they are not easily recognisable in the living individual, especially not in many of the constricted forms.

They come apart, however, during conjugation (figs. 106 B; 110) and sometimes after death; separation can often also be induced by treatment with alkalies. The mature wall is further composed of two well-differentiated layers. The inner one is structureless and consists mainly of cellulose; the outer is firmer and thicker and is composed of a basis of cellulose impregnated with various other substances (pectic substances according to van Wisselingh (196)) which often include iron-compounds. These are most prominent in some species

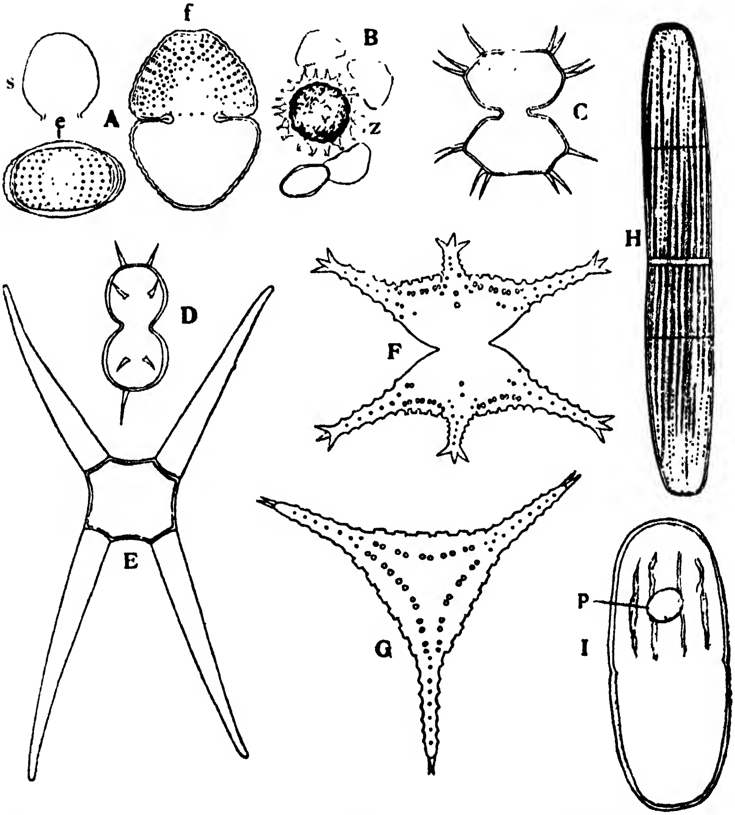

Fig. 106. A, B, *Cosmarium tetraophthalmum* Bréb. var. *Horwoodii* Rich; B, zygospore. C, D, *Xanthidium controversum* West; D, side-view. E, *Closterium rostratum* Ehrenb. var. *brevirostratum* West, zygospore. F, G, *Staurastrum anatinum* Cooke and Wills; G, end-view. H, *Penium spirostriolatum* Barker. I, *P. polymorphum* Perty. *e*, end-view; *f*, front-view; *p* pyrenoid; *s*, side-view; *z*, zygospore. (A, B after Rich; I after Borge; the rest after West.)

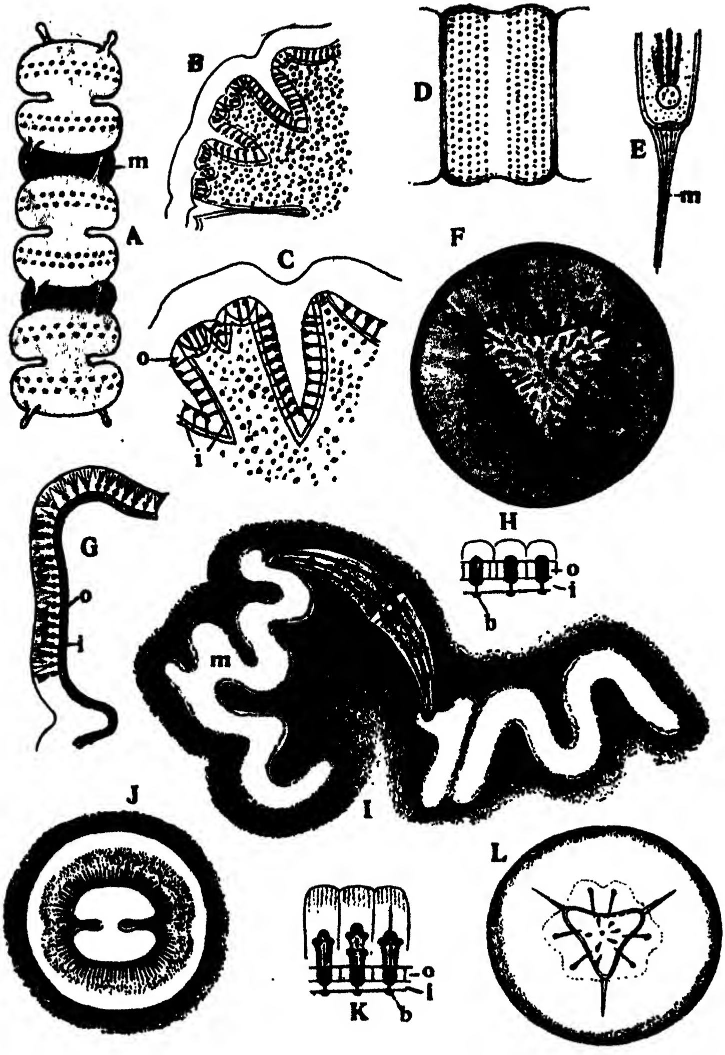

Fig. 107. Wall-structure of Desmids. A, *Onychonema filiforme* (Ehrenb.) Roy & Biss. B, C, *Micrasterias crux-melitensis* (Ehrenb.) Hass., pore-organs. D, *Hyalotheca dissiliens* (Sm.) Bréb. E, *Closterium didymotocum* Corda. F, *Staurastrum pseudofurcigerum* Reinsch, pore-organs and mucilage-envelope. G, *Micrasterias denticulata* (Bréb.) Ralfs, wall with pore-organs

of *Closterium* and *Penium*, where the membranes exhibit a yellowish or yellowish brown colour, but localised deposition of iron is met with in many other Desmids (76), although lacking in the Mesotaeniaceae. The cell-wall sometimes contains traces of silica. The outer layer of the wall frequently bears granules, spines, warts, or other protuberances, most of which show a definite arrangement (cf. fig. 106 A). The genus *Xanthidium* (fig. 106 C, D) is essentially characterised by the simple or forked spines borne at the angles of the semicells.

External to the outer layer of the wall there is nearly always a thin diffluent mucilaginous coat, but in some Desmids this is more strongly developed, completely surrounding the individual or in colonial forms the colony; this mucilage is frequently the home of foreign organisms (including Bacteria). It is by means of the mucous envelope that Desmids adhere to other larger aquatic plants, and sometimes, when rapid multiplication has taken place, numerous individuals occur embedded in such masses of jelly. In some cases the mucus is tough, as for instance when it forms the pads or processes by means of which the individuals are connected in the filamentous colonies (fig. 107 A, *m*).

The mucilage is secreted through pores (72, 86, 107, 152) which traverse the wall and are not uncommonly clearly visible without special treatment; they appear to be absent in *Penium* and some small species of *Cosmarium*. In several genera the pores are almost uniformly distributed over the wall (e.g. *Micrasterias*, fig. 107 B, C) except that they always appear to be lacking in the region of the isthmus (fig. 107 D). In richly ornamented forms, like many of the species of *Cosmarium*, they are commonly grouped symmetrically around the bases of the spines, warts, etc., of the outer layer of the wall. In *Closterium* (105) they are usually arranged in longitudinal rows in the narrow grooves between the fine ridges with which the membrane is often provided (fig. 109 L).

In the inner layer of the wall the pore is a simple canal, but in the outer layer the canal is surrounded (in all genera except *Closterium*) by a specially differentiated cylindrical zone, not composed of cellulose (cf. fig. 107 H, K, *o*). This has been termed a "pore-organ" by

and mucilage-envelope. H, *Cosmarium turgidum* Bréb., pore-organs. I, *Closterium moniliferum* Ehrenb., secretion of polar mucilage-masses, cell in sepia. J, *Cosmarium subtumidum* Nordst., mucilage-envelope with three layers. K, *Xanthidium armatum* (Bréb.) Rabenh., pore-organs. L, *Staurastrum lunatum* Bréb., forma, pore-organs and mucilage-envelope. *b*, internal enlargement of pore-organ; *i*, inner and *o*, outer part of membrane; *m*, mucilage. (A, H, K after Lütkemüller; D, E after Klebs; the rest after Schröder.)

Lütkemüller (107) who investigated these structures most fully. The canals are no doubt in all cases occupied by threads of mucilage (cf. however (72)) in process of excretion. At the inner surface of the wall these threads often terminate in lens- or button-shaped swellings (fig. 107 H, K, *b*), whilst at the outer limit of the pore-organ there are often similar dilations, sometimes complex in form (fig. 107 K) and in a few cases giving rise to a delicate radiating mass of mucilage (fig. 107 G). These diverse structures are apparently more or less permanent in character. In many of the larger Desmids there are numerous smaller pores between the larger ones and confined to the outer layer of the wall.

The envelope of mucilage is readily stained by dilute methyl violet and, as Schröder (152) showed, can usually be demonstrated by placing the cells in diluted Indian ink for which the mucus has no affinity. This envelope often (except *Closterium*, *Arthrodesmus*) exhibits a prismatic or fibrillar structure (fig. 107 J), especially in the inner region. This structure no doubt corresponds to the exudation of mucilage through the individual pores in the form of a number of closely apposed prisms (cf. also fig. 107 F). Where special mucilage-masses are recognisable external to the pore-organs, each of these occupies the middle of one of the prisms.

The slow movements frequently exhibited by Desmids,[1] when in contact with a substratum, are due to local exudation of mucilage. The latter is usually excreted through specially large pores situated near the ends of the cells (fig. 107 E), and irregular worm-shaped masses, two or three times the length of the individual, may be secreted at these points in the space of an hour (fig. 107 I). In *Closterium* the cells often perform pendulum-like movements about one fixed extremity; sometimes the free end swings through 180° to become attached in its turn, whilst the other repeats the movement. Thus, by a series of somersaults, each occupying 6–35 minutes according to the temperature, the cell moves forward over the substratum. In other genera the movements seem more erratic. As directional stimuli light and gravity come into play.

The desmid-cell always has a single nucleus which is usually embedded in a small median mass of cytoplasm in the region of the isthmus (figs. 105 G; 108, *n*). The chloroplasts have been investigated by various workers (17, 104, 149). In the vast majority of cases they are axile and one occupies each semicell (fig. 108 G, K). Two chloroplasts, however, occur in each semicell in many species of *Cosmarium* (fig. 108 B, C), in *Euastrum verrucosum*, and a few species of *Xanthidium* (fig. 108 H). Such axile chloroplasts typically consist of a central piece, which is rod-shaped in elongate forms like *Closterium* (figs. 105 G; 108 A, G) and *Penium*, although usually more or less

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[1] See (85), (86), (90), (152), (160), (161).

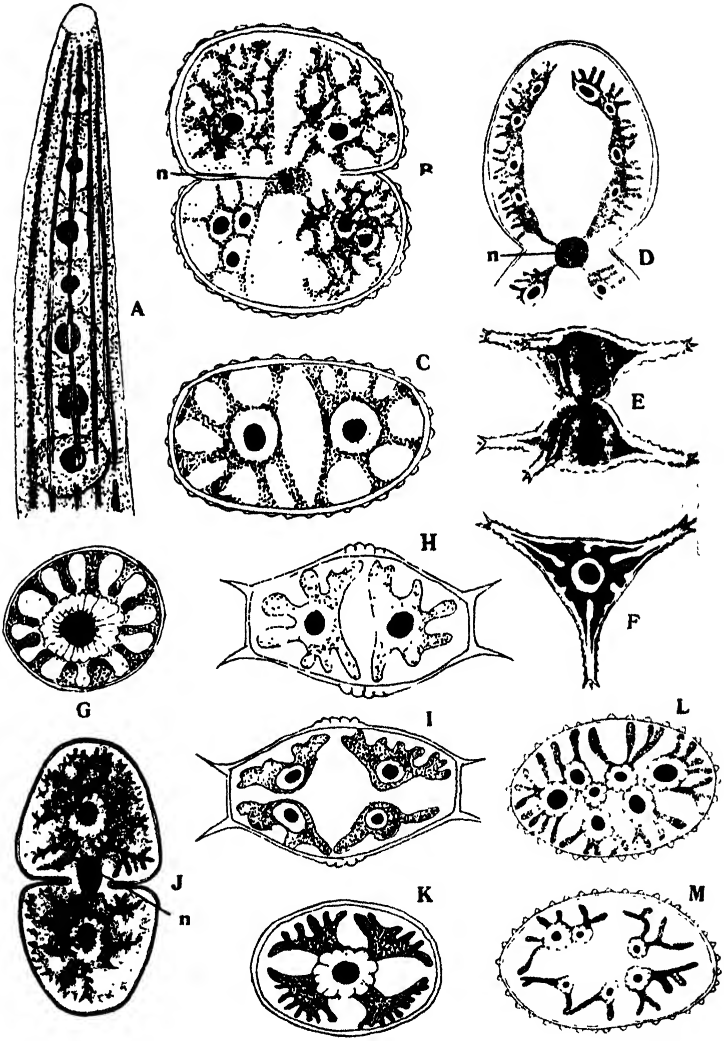

Fig. 108. Chloroplast-structure in Desmids (after Carter). A, G, *Closterium lanceolatum* Kütz.; G, transverse section. B, C, *Cosmarium reniforme* (Ralfs) Arch.; C, optical transverse section. D, *C. ovale* Ralfs, optical longitudinal section. E, F, *Staurastrum Manfeldtii* Delp.; F, end-view. H, I, *Xanthidium Brebissonii* Ralfs, transverse sections of two individuals. J, K, *Cosmarium pseudopyramidatum* Lund.; K, optical transverse section. L, M, *C. Brebissonii* Menegh., transverse sections of two individuals. *n*, nucleus.

rounded in other genera; from this axial portion there arise a number of plates or processes which extend towards the periphery of the cell. In *Closterium* (fig. 108 A) the elongate chloroplast in each semicell bears more or less numerous longitudinal ridges which are sometimes undulate or anastomose with one another.[1] The axile chloroplasts of *Staurastrum* (fig. 108 E, F) bear a number of bilobed extensions, one of which penetrates into each angle of the semicell.

There is a clearly recognisable tendency in many, and especially the larger, species of *Cosmarium*, *Euastrum*, etc., for the ends of the chloroplast-processes to spread out into parietal, sometimes richly lobed or fringed, plates within the bounding cytoplasmic layer of the cell (fig. 108 J, K), and the extent of this parietal development may vary considerably in one and the same species. In *Cosmarium Brebissonii* Menegh. some individuals have elaborate axile chloroplasts (fig. 108 L), whilst others have no axile system at all and instead possess a number of parietal chloroplasts (fig. 108 M). In quite a number of Desmids (e.g. *Cosmarium ovale* Ralfs, fig. 108 D; *Staurastrum tumidum* Bréb.; many species of *Xanthidium*, fig. 108 I; and *Pleurotaenium*) the chloroplasts are solely parietal and occur as a number of bands in each semicell. In *Pleurotaenium* the bands are sometimes broken up into numerous pieces, each with one pyrenoid. All the evidence points to a close relation between the two types of chloroplast-structure, the parietal system being probably a later development than the axile one and apparently often arising *pari passu* with an increase in the size of the cell. In the genus *Cosmarium* closely related species are sometimes mainly distinguished by respective parietal and axile arrangement of the chloroplasts (e.g. *C. subcucumis* Schmidle and *C. cucumis* Corda).

In Desmids having axile chloroplasts the pyrenoids are usually located in the central portion (fig. 108 F, G, H, K). In *Closterium* (fig. 108 A), and sometimes in *Penium*, there is a row of pyrenoids, in other cases a single one. Carter ((17) pp. 215, 295, etc.) and Ducellier (50) have, however, drawn attention to the frequent multiplication of the central pyrenoid (fig. 108 B), although, since the products of its division often remain close together, this may be difficult to recognise except in carefully fixed and stained specimens. This multiplication probably shows the way in which the scattered pyrenoids found in the chloroplasts of some forms have arisen; this condition is met with in *Closterium Ehrenbergii*, many species of *Euastrum*, and occasional species of *Cosmarium* (fig. 108 L) and *Staurastrum*. A number of pyrenoids are also usually found in each of the parietal chloroplasts above mentioned (fig. 108 D, M). Carter ((17) p. 226) further records in a considerable number of the species

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[1] The account given by Lutman (111) is probably scarcely typical for the genus.

examined by her small naked pyrenoids devoid of a starch-sheath and such may be met with in the peripheral processes when the ordinary pyrenoids are restricted to the axial portion.

In Desmids with large axile chloroplasts vacuoles may be absent or of small size, but in those with parietal chromatophores large vacuoles are often present in the central parts of the cell. In *Closterium* and *Pleurotaenium* there is a well-marked terminal vacuole at each extremity of the individual (cf. fig. 109 H, K, *v*), containing one or many vibrating crystalline bodies of irregular or definite shape, the number always being the same in the two vacuoles of an individual, but not being a constant for the species (54, 55, 93, 154). In *Closterium* they are believed to be minute crystals of gypsum, and they are stated to be formed in the cytoplasm and subsequently to become transferred to the vacuoles ((54) p. 149, (93) p. 294). Their movements cease with the death of the cell. According to Steinecke (164) the crystals always lie against that wall of the vacuole which is directed downwards and he therefore regards them as statoliths, a conclusion against which several other investigators have pronounced. Certain mucilaginous bodies commonly found in the ordinary vacuoles of *Pleurotaenium* and sometimes in *Cosmarium* are of unknown significance (54, 92). Circulation of the cytoplasm is often obvious in the larger forms (*Closterium*, etc. (6, 54, 154, 190)).

CELL-DIVISION

The usual method of multiplication is by cell-division, and in many species this would appear to take place indefinitely without conjugation occurring. The process of cell-division is complicated by the bipartite structure of the wall and some points relating to it still remain obscure. Division occupies about a day in the smaller, several days in the larger species.

In a simple unconstricted form like *Hyalotheca* ((72) p. 46) the process shows much resemblance to that found in species of *Microspora*, division being initiated by the development of a cylindrical strip of membrane on the inner side of the wall at the level of the junction of the two semicells. The septum arises from this as an annular ingrowth (fig. 109 D) and when complete splits into two, whereby each individual acquires a new semicell which gradually enlarges to its full size; the other semicell is derived from the parent. In Desmids with a marked median constriction (e.g. *Cosmarium*)[1] the first step is an elongation of the isthmus, causing a slight separation of the two semicells. This is followed by the development, within the region of the isthmus, of a cylindrical strip of membrane whose mode of origin is not altogether clear. From this strip a transverse septum

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[1] See (6), (72), (107) p. 360.

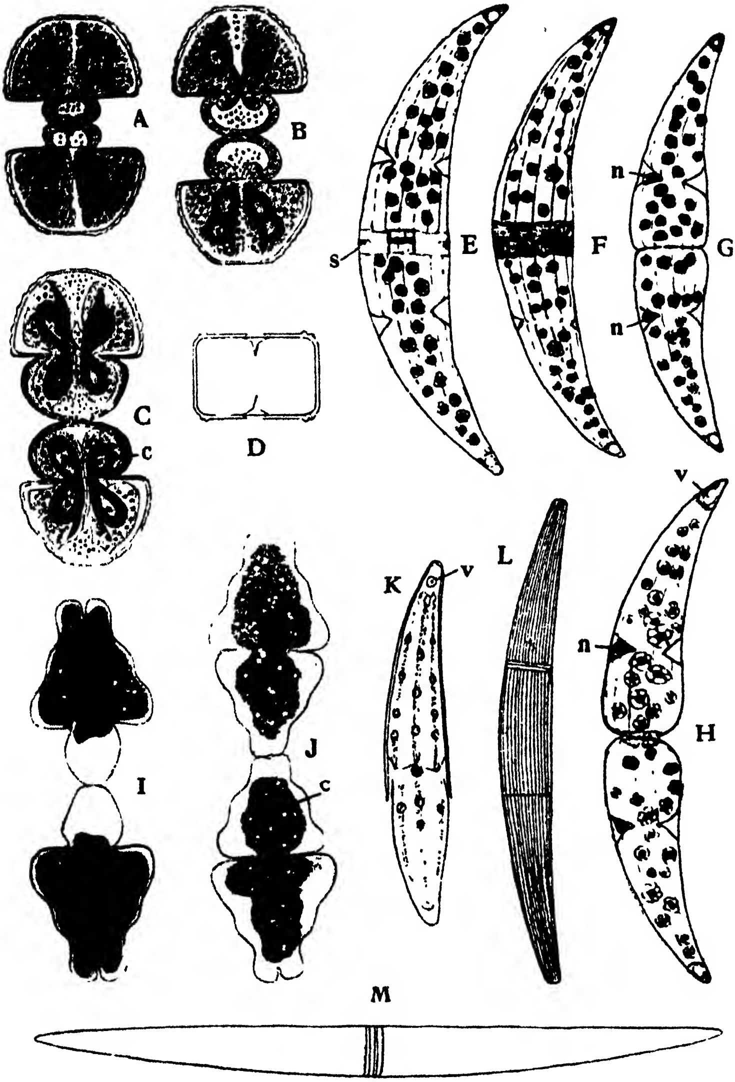

Fig. 109. Cell-division in Desmids. A–C, *Cosmarium botrytis* Menegh. (after De Bary). D, *Hyalotheca mucosa* (Mert.) Ehrenb. (after Hauptfleisch), formation of septum. E–H, *Closterium Ehrenbergii* Menegh. (after Lutman); E, nucleus in metaphase, septum-formation commencing; F, septum nearly

develops, demarcating the two new halves and later splitting into two. The young semicells gradually enlarge (fig. 109 A–C, I, J), but usually remain in contact by their apices until they are practically fully grown.

According to Lütkemüller ((107) p. 362) the membrane of the new semicells is always quite smooth (cf. fig. 109 C) and a second membrane provided with the ornamentation typical for the species develops on its inner side, after which the primary one is cast off. In his opinion this is the rule in constricted Desmids, although not occurring in the colonial forms. The matter is worthy of a fresh investigation.

The cell-division of *Closterium* is of rather a different type;[1] it has been specially investigated by van Wisselingh (196) and Lütkemüller (107, 110) whose conclusions are, however, at variance. A first peculiarity lies in the fact that the dividing wall is not formed at the boundary between the two semicells, but a little way beyond in the younger semicell. At this spot the outer layer of the wall is lacking, while the inner layer is thickened so as to project slightly into the cell-cavity (fig. 109 *bis*, C, *r*); a slight external constriction ("Ringfurche"), appearing superficially as a transverse line (fig. 109 *bis*, A, *r*), marks the point at which this special structure occurs. When division is about to take place, this local thickening becomes drawn out into a cylindrical strip owing to a slight elongation of the cell, and from this new segment of the wall a septum grows inwards (cf. fig. 109 F) in the same way as in *Hyalotheca*. It is at this point that the interpretations diverge. According to Lütkemüller the septum later splits and the two halves become bulged out to form the new semicells of the respective daughter-individuals (fig. 109 K). The individual which receives the older semicell of the parent will thus possess a narrow *connecting band* (fig. 109 *bis*, A, III, *c*) extending between the suture (*s*) marking the connection between the two halves of the parent-cell and that marking the connection between the old and new semicells (*t*). Each division will add a further connecting band to the daughter-individual that acquires the older semicell. In this way the series of fine transverse lines to be seen in the equatorial region of many species of the genus originate (cf. fig. 109 M).

According to van Wisselingh, after formation of the septum, a complete layer of cellulose is deposited over the whole inner surface of the wall in each daughter-individual and, as the septum splits, this layer bulges out to form the new semicell. On his interpretation

[1] The account of Fischer (53) is not correct in all its details.

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complete; G, new ends beginning to round off, nuclei at constrictions of chloroplasts; H, later stage. I, J, *Euastrum Didelta* (Turp.) Ralfs (after Carter). K, *Closterium Leibleinii* Kütz. (after Steinecke). L, *C. striolatum* Ehrenb. (after West), with girdle-band. M, *C. acerosum* (Schrank) Ehrenb. (after West), showing connecting bands. *c*, chloroplast; *n*, nucleus; *s*, septum; *v*, terminal vacuole.

the wall of a *Closterium*-cell consists of one piece as far as the inner strata are concerned, but the older semicell will have several external strata overlapping one another and stopping short at various points, their limits marking the limits of the connecting bands.

In a number of species of *Closterium* (e.g. *C. intermedium* Ralfs, *C. striolatum* Ehrenb., fig. 109 L) the wall shows special structures known as *girdle-bands*, of which there are never more than two. They arise (cf. fig. 109 *bis*, B) by the development of an internal thickening of the wall in the younger semicell, a little way from its point of junction with the older one; at this point the cell-membrane ruptures transversely and the girdle is formed (fig. 109 *bis*, B, I *a*) by stretching of the thickening ring between the ruptured portions (Lütkemüller) or by the stretching of a complete cellulose-layer apposed to the whole inner surface of the wall (van Wisselingh). The formation of a girdle is of course also accompanied by the production of an additional connecting band (cf. fig. 109 *bis*, B, II *a*, *c*). In a few species of *Penium* (e.g. *P. spirostriolatum* Barker, fig. 106 H) similar girdle-bands are formed. These phenomena recall in many ways the mode of growth of the wall of *Oedogonium* ((139) p. 345).

Certain complications in the division-process are also seen in the colonial genera *Desmidium* and *Gymnozyga* (*Bambusina*). Here the septa soon after their formation, after splitting into two in the usual way, develop on either side a cylindrical ring-like ingrowth (fig. 114 D, D′, *r*), similar to that found in species of *Spirogyra* with replicate end-walls. As the young semicells enlarge, these invaginations become protruded to form their contiguous apices ((6) p. 44, (72)) (fig. 114 D).

The young semicells are usually clearly recognisable and nuclear division is complete before any change takes place in the chloroplasts of the parent (fig. 109 A, I). At a certain stage, however, the chloroplasts commence rapidly to enlarge and extend through the isthmus from the old into the new semicell (fig. 109 C, J) so that, when the latter reaches its full size, it is generally completely occupied by them. Division of the chloroplasts then occurs at the isthmus (6, 17). In *Closterium*, however, according to Lutman (112), constriction of the chloroplasts commences before any other changes are apparent (fig. 109 E). After nuclear division is completed the daughter-nuclei move to the points of constriction of the chloroplasts and there take up their normal position within the young individuals (fig. 109 G, H).[1]

THE PROCESS OF CONJUGATION

In the process of conjugation (6) two individuals become approximated and enveloped by mucilage; in the Cosmarieae they are not uncommonly placed at right angles to one another (fig. 110 A–C). In

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[1] Regarding nuclear division in Desmids, see (112), (195). See also No. 1 on p. 75.

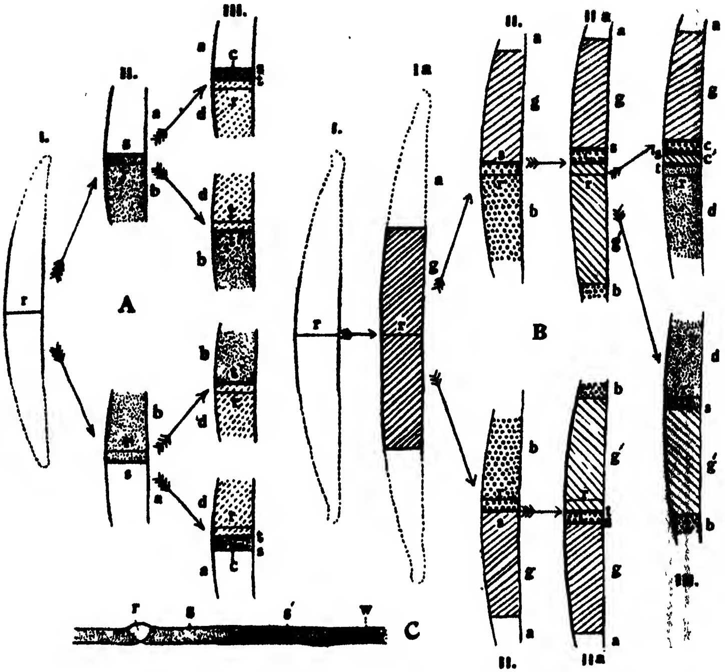

Fig. 109 *bis*. Diagrams to explain cell-division in species of *Closterium* with (B) and without (A) girdle-bands (modified from Lütkemüller). The different segments of the wall are indicated by distinctive shading. I, II, III, the successive generations. C, part of membrane of *C. turgidum* Ehrenb. in section (after Lütkemüller). The individual I in A is supposed to result from a zygote, has a membrane in one piece, and has not yet undergone division; it shows near its middle a faint line (*r*) marking the internal thickening of the wall (the future point of division). In II each individual shows the suture (*s*) between the older and younger (dotted) semicells and, within the latter, the line *r* marking the next point of division. In III one of each pair of individuals arising from the division of II possesses a connecting band (*c*) composed of a short strip of the wall of the younger semicell of II, such a connecting band being demarcated by two lines, one (*s*) the suture of the previous generation, the other (*t*) the suture demarcating the old and new semicells. In B three successive generations are likewise shown arising from the individual I which is supposed to have originated from a zygote. This individual is supposed first to develop two girdle-bands (*g* in I *a*) then to divide (II), each such individual producing a further girdle-band (II *a*, *g*′) before dividing again (III). *a*, *b*, *d*, three semicells of successive ages; *c*, connecting bands; *c*′, connecting band derived from girdle-band; *g*, girdle-bands; *r*, in all cases the line due to the internal thickening of the wall marking the next point of division; *s*, *t*, sutures between semicells of different ages; *w* in C, the main wall of the semicell; *s*, *s*′ in C, segments of the wall.

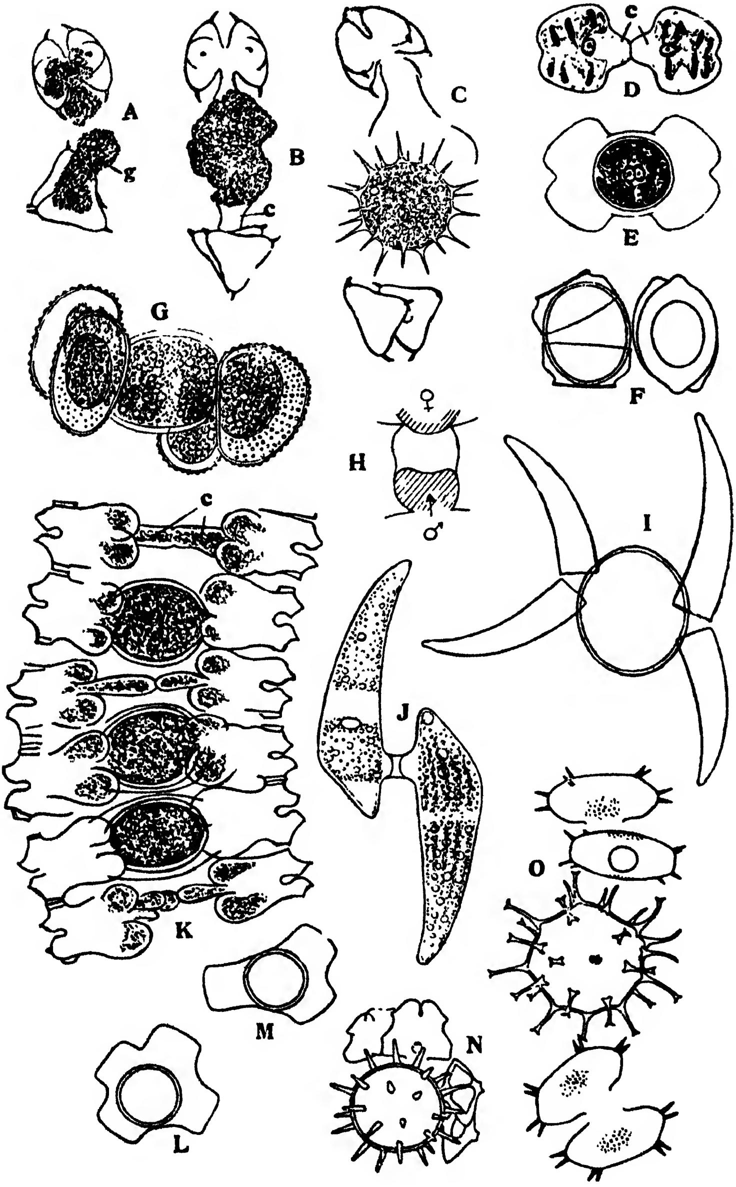

Fig. 110 [*for description see opposite*]

many Desmids the semicells of each individual merely come apart at the isthmus and the protoplasts are set free and fuse (fig. 110 G, N, O). In some cases (*Closterium*, fig. 110 J; *Desmidium*, fig. 110 K; *Hyalotheca*, fig. 110 D, etc.), however, more or less distinct protuberances of variable size arise from the isthmus of each conjugating cell and join to form a tube within which fusion occurs. In *Closterium Ehrenbergii* these conjugating processes are stated ((148) p. 142) to grow out of a rounded aperture that arises in the membrane of each copulating individual. According to Pothoff (135) the protuberances in *Hyalotheca* (fig. 110 D) in most cases only arise from cells in contact with each other (cf. Zygnemoideae).

In most of the filamentous types dissociation into the individual cells occurs prior to conjugation (fig. 110 D, E, F, M), exceptions being found in certain species of *Desmidium* (e.g. *D. Swartzii*, fig. 110 K). The zygospore is formed between the conjugating cells, with the sole exception of *Desmidium cylindricum* Grev. (6, 153) where it is lodged within the female cell (fig. 110 F). According to Scherffel (148) in *Closterium parvulum* one protoplast passes into the conjugation-canal sooner than the other (fig. 110 H) which probably implies a sexual differentiation. As an abnormality three or even four desmid individuals may participate in the formation of a zygospore.

It frequently happens that conjugation ensues between young individuals soon after division (6, 182, 184) and before the new semicells have arrived at maturity (fig. 110 J). This has led to the view that conjugation takes place between recently formed daughter-individuals, but for this there is no very satisfactory evidence (cf. (89)). Conjugation between adjacent cells of filamentous forms (i.e. lateral conjugation) has been observed in species of *Sphaerozosma* and *Spondylosium* (p. 357), as well as in *Hyalotheca* (135), but such cases are very rare. It is unlikely that conjugation between different species will often occur, in view of the rarity of the process in Desmids; in fact only one example of the kind has been recorded (5).

Double zygospores (cf. p. 314), formed by the conjugation of pairs of recently divided individuals, are met with as an occasional phenomenon in a number of species (e.g. *C. Ehrenbergii*, fig. 111 D, cf. (6),

Fig. 110. Sexual reproduction in Desmids. A–C, *Staurastrum Dickiei* Ralfs; A, liberation of gametes; B, fusion; C, zygote. D, E, L, M, *Hyalotheca dissiliens*; D, conjugation; E, zygote with two nuclei; L, M, zygospores. F, *Desmidium cylindricum* Grev., zygospore in one conjugating cell. G, *Cosmarium botrytis*, conjugation. H, I, *Closterium parvulum* Naeg., H, anisogamy; I, zygospore. J, *C. Ehrenbergii*, conjugation. K, *Desmidium Swartzii* Ag., var., conjugation. N, *Euastrum elegans* (Bréb.) Kütz., zygospore. O, *Xanthidium antilopaeum* (Bréb.) Kütz., zygospore. *c*, conjugation-process; *g*, gamete. (D, E after Pothoff; G, J after De Bary; H after Scherffel; K after Turner; the rest after West.)

(148), (159 a)), but their production is the rule in certain others. In *Penium didymocarpum* Lund. (fig. 111 A, B) the paired zygospores are stated to be formed by conjugation between four cells produced by two consecutive divisions of one individual. In *Closterium lineatum* Ehrenb. (fig. 111 C, E) and certain other species of the genus, each zygospore arises from the union of a pair of gametes, one produced from a semicell of each individual.

The formation of what are possibly to be regarded as parthenospores[1]

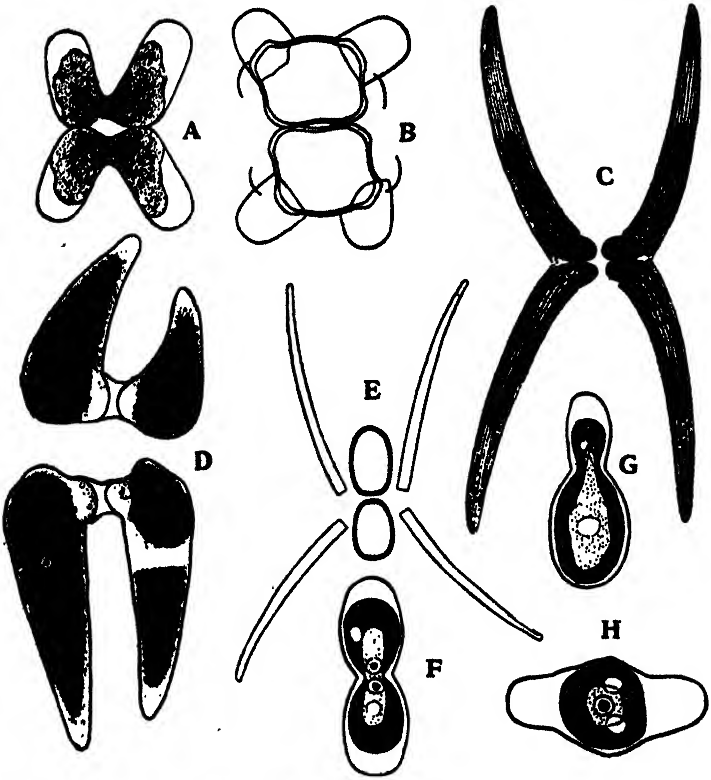

Fig. 111. A, B, *Penium didymocarpum* Lund.; A, conjugation of four individuals just produced by division; B, completed conjugation, double zygospores. C, E, *Closterium lineatum* Ehrenb.; C, early conjugation (diagrammatic); E, double zygospore. D, *C. Ehrenbergii*, two recently divided individuals in conjugation. F–H, *Chlamydomonas eugametos* Moewus; F, isogamous and G, anisogamous fusion; H, rounding off of zygote. (C after Oltmanns; D after Scherffel; F–H after Moewus; the rest after West.)

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[1] Some of these afford a rather abnormal impression.

has been observed very occasionally in diverse Desmids (78, 122, 184), and Klebs (87) was able to induce their formation experimentally in *Closterium Lunula* and *Cosmarium botrytis*.

The mature zygospores appear usually to have a membrane of three layers, of which the inner is thin and colourless, the middle one firm and often brown-coloured, and the outer either smooth (fig. 110 E, L, M) or covered with variously arranged warts or spines (fig. 110 C, N, O) which in the advanced forms are often repeatedly branched. Such spines develop as thin-walled protrusions of the membrane and remain hollow until all the branches are formed (88). In *Hyalotheca* (fig. 110 L, M) the walls of the conjugating cells remain firmly connected with the conjugation-canal in which the zygospore is formed. Wherever the matter has been investigated fusion of the gamete nuclei is delayed until just prior to germination which takes place after a prolonged resting period. The chloroplasts of the gametes usually become indistinct during conjugation, but in the mature zygotes two chlorophyll-containing masses are often recognisable. According to Kauffmann ((83) p. 764) two of the four chloroplasts of the gametes disintegrate during the maturation of the zygospores of *Penium*, *Closterium*, and *Staurastrum*, while in *Hyalotheca* one of the two disorganises (135) and this may well be general (cf. also (136) p. 671).

The details of germination are only known in a few cases (6, 84, 118). As in other Conjugales two successive nuclear divisions (fig. 112 B–D) take place in the germinating zygote, of which the first is the reduction division (cf. (135), (136)). Thereupon the contents, which have escaped from the outer envelopes of the spore, divide into two individuals (fig. 112 E, G), each of which in *Closterium* contains one chloroplast and two nuclei, one of which enlarges while the other gradually disappears (fig. 112 E, F). The production of two individuals would seem to be the rule in Desmids, but in some cases (175) there are four (fig. 112 J), while in *Hyalotheca dissiliens* (fig. 112 K, L) there is only one (135). In the last case two of the four nuclei at first enlarge (fig. 112 K), but one of these aborts in addition to the two smaller ones. The first-formed cells are devoid of the characteristic markings of the species (fig. 112 H), but these are acquired by the new semicells after the first vegetative division (fig. 112 I). The germinating parthenospores of *Cosmarium* likewise exhibit a formation of four nuclei, but only one survives by contrast to the zygospores (84).

THE EVOLUTIONARY SEQUENCE IN DESMIDS

In no other group can evolutionary series be so clearly recognised as among Desmids, and there is abundant evidence of parallel development (58). Whatever view one may take as to the origin of the group

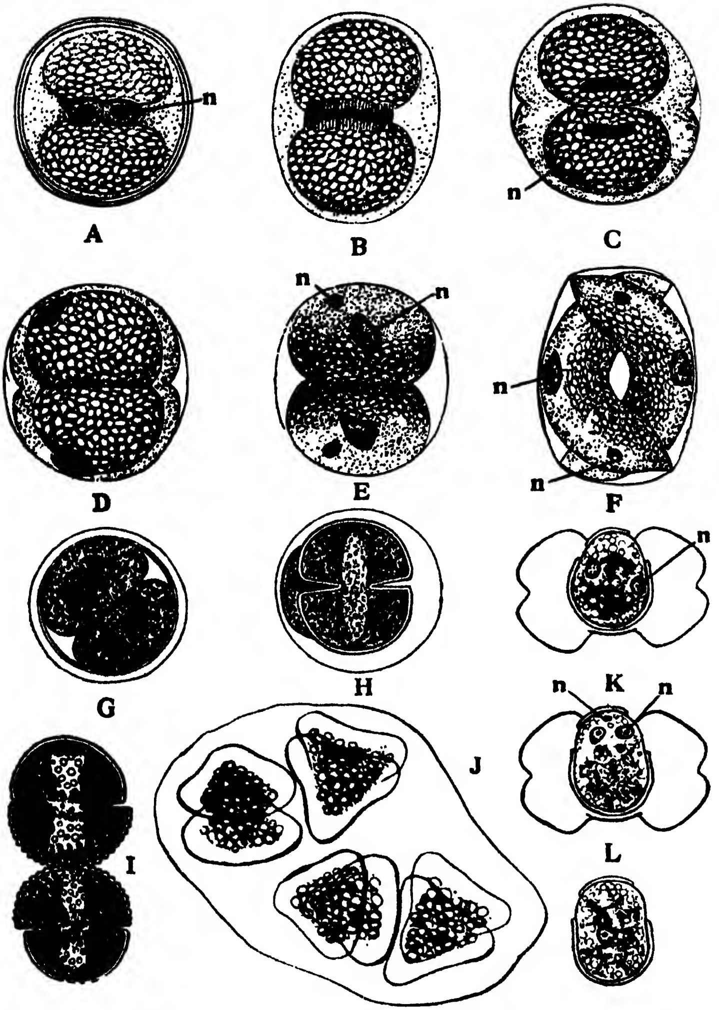

Fig. 112. Germination of the zygote in Desmids. A–F, *Closterium* sp. (after Klebahn); A, zygote with two nuclei; B, first nuclear division in escaped contents; C, binucleate stage; D, second nuclear division; E, degeneration of two nuclei; F, young individuals. G–I, *Cosmarium botrytis* (after De Bary); G, H, differentiation of two individuals; I, products of the first division of one of these (note the smooth semicells). J, *Staurastrum Dickiei* var. *parallelum* Nordst. (after Turner), germinating zygote with four individuals. K, L, *Hyalotheca dissiliens* (after Pothoff); K, above first nuclear division completed, below abortion of two of four nuclei; L, surviving individual with single nucleus. *n*, nucleus.

(cf. p. 361), the ancestors must have possessed cells with the general shape of those of the Mesotaenioideae, i.e. they will have had rounded semicells devoid of a median constriction and circular in cross-section. Such cells are indeed characteristic of many species of *Penium* (fig. 106 H, I) among the Desmidioideae and, in a somewhat more specialised form, are seen also in *Closterium*, *Pleurotaenium*, etc. In the further evolution of the desmid-cell there occurred constriction and flattening, both barely indicated in some of the simpler species of *Cosmarium*, but much more pronounced in those exhibiting elaboration of form or ornamentation (figs. 106 A; 108) and especially evident in genera like *Euastrum*, *Xanthidium* (fig. 113 I–K), and *Micrasterias*, which attain to some of the most complex outlines (cf. fig. 113 G) known in the group.

Flattening of the cell results in a usually elliptic vertical view (fig. 113 A, N), but in a large number of the *Cosmaria* the ellipse shows a more or less marked median swelling, due to the dilation of the face of the semicell above the isthmus (fig. 113 U); this swelling often bears a distinctive ornamentation. In certain species of *Cosmarium* (e.g. *C. Holmii* Wille) these swellings may attain to such dimensions that the outline of the cell in end-view comes to be quadrangular (fig. 113 A–F), so that these forms can with equal justification be referred to *Staurastrum* ((103) p. 29). Such median swellings are a marked feature of most species of *Euastrum* and *Xanthidium* (fig. 113 K), and there can be no doubt that they represent a further specialisation of the desmid-cell.

Whilst a direct derivation of the staurastroid type from *Cosmarium*-like forms along the lines just indicated is probable, it would scarcely appear to be the normal mode of origin of species of *Staurastrum*, since in the vast majority the triangular end-view preponderates (figs. 105 F; 106 F, G), the quadrangular one being on the whole rather rare. The tendency to evolve forms with a triangular end-view is, however, widespread among Desmids, being known for quite a large number of species of *Cosmarium* (fig. 113 L) and a few species of *Xanthidium* and *Arthrodesmus*; moreover, such forms are even found in three species of the highly specialised genus *Micrasterias* (fig. 113 H), while the peculiar tropical genus *Euastridium* (180) appears to represent the same tendency on the part of euastroid forms. The fact that species with a triangular end-view are rather frequent in the genus *Cosmarium* no doubt indicates that the origin of most species of *Staurastrum* is to be sought among those of this genus. Many of the less specialised types of *Staurastrum* are indeed closely parallel to species of *Cosmarium*.

The general evolutionary trend among Desmids, in passing from the simpler to the more complex individuals, is also recognisable with respect to the features of conjugation. The simpler forms have

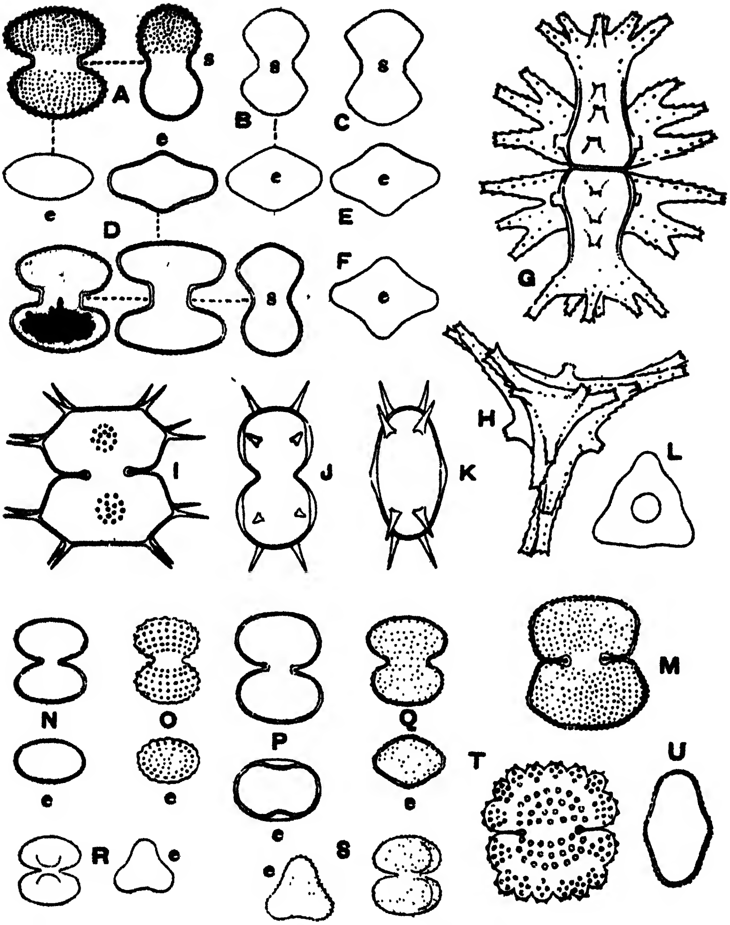

Fig. 113. A–F, *Cosmarium Holmii* Wille, various individuals; note the diverse character of the end-views. G, H, *Micrasterias mahabuleshwarensis* Hobs. var. *Wallichii* (Grun.) West; H, the triquetrous end-view. I–K, *Xanthidium antilopaeum* (Bréb.) Kütz.; J, side- and K, end-views. L, M, U, *Cosmarium biretum* Bréb.; L, end-view of forma *triquetra* Bréb.; U, usual end-view. N–S, series illustrating evolution of ornate and staurastroid forms; N, *C. contractum* Kirchn. var. *ellipsoideum* West; O, *C. portianum* Arch. var. *orthostichum* Schmidle; P, *C. foveatum* Schmidle; Q, *C. scabratulum* West; R, *Staurastrum muticum* Bréb.; S, *S. turgescens* De Not. T, *Cosmarium caelatum* Ralfs. *e*, end-view; *s*, side-view. (A–F after Lowe; G, H after Homfeld I after Ralfs; P after Borge and Schmidle; the rest after West.)

smooth spherical zygospores, while the more complex have spores provided with an armature of simple or forked spines. Moreover, there is clearly a tendency for elimination of the conjugation-process in the more advanced types. While zygospores are known for a large proportion of the simpler Desmids, in many of which too the production of zygospores appears to take place with great frequency, the specialised types appear not only to produce zygospores rarely, but in many of them (even in common, widely distributed species) conjugation has as yet not been noted.

It is a well-known fact that, whilst there is no difficulty in referring the majority of Desmids to their appropriate genus, there are a considerable number of species which one must regard as border-line forms whose reference to one or other genus is largely a matter of personal opinion. In other words most of the genera merge into one another. Moreover, when one surveys the numerous species of Desmids that are known, it becomes apparent that a considerable number of lines of parallel evolution are recognisable. Thus, starting with a number of species of *Cosmarium* showing diverse shapes in front-view, but all possessing smooth membranes and a circular or simple elliptical end-view, we can distinguish for each such simple form (fig. 113 N) one or more of the following specialised types: (*a*) the same form with an ornamented membrane (fig. 113 O); (*b*) the same form with a median swelling in end-view (fig. 113 P); (*c*) the same form with a median swelling and an ornamented membrane (fig. 113 Q); (*d*) a staurastroid modification with a smooth membrane (fig. 113 R); (*e*) a staurastroid modification with an ornamented membrane (fig. 113 S). A considerable number of such parallel series can be picked out without much difficulty, and they display very plainly the lines along which evolution in this group has taken place. The sigmoid shapes not uncommonly assumed by various species of *Closterium* exemplify a similar parallelism (46).

The close relation between the different genera of Desmids is demonstrated by the fact that it is not possible to classify them in more than a single family, Desmidiaceae, among which the three tribes Penieae (with *Penium*), Closterieae (with *Closterium*) and Cosmarieae (comprising all the remaining genera) are usually distinguished.

The majority of the colonial Desmids are evidently closely related to the non-colonial types. Thus, *Sphaerozosma* (fig. 114 F) and *Spondylosium* (fig. 114 A) are clearly colonial forms of the *Cosmarium*-type, while the cells of *Desmidium* (fig. 114 B, C) show the angular end-views and the chloroplasts of a *Staurastrum*. Filamentous colonies are, moreover, occasionally met with in species of *Cosmarium*, *Euastrum*, *Micrasterias*, etc. In the majority of the filamentous Desmids the cells are connected by mucilage-pads developed between

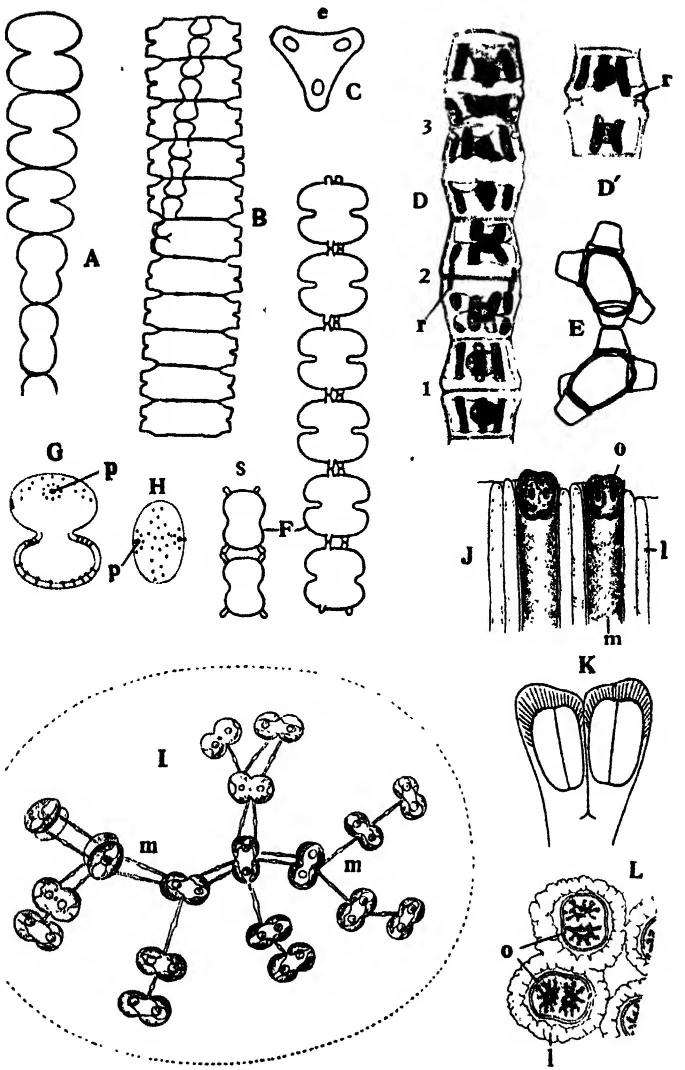

Fig. 114. Colonial Desmids. A, *Spondylosium ellipticum* West. B, C, *Desmidium Swartzii* Ag. D, D′, *Gymnozyga Brebissonii* Kütz., mode of growth of cell; D′, a stage between *1* and *2* in D. E, *G. moniliformis* Ehrenb., var. *gracilescens* Nordst., two zygospores. F, *Sphaerozosma vertebratum* Ralfs. G–I, *Cosmocladium saxonicum* De Bary; G, H, distribution of mucilage-

their contiguous faces, but in *Sphaerozosma* (fig. 114 F), for instance, they are joined by short apical processes. Whilst most of the colonial Desmidiaceae are filamentous, other types occur in *Cosmocladium* and *Oocardium*.

In the former (151) the *Cosmarium*-like cells are united to form branched microscopic colonies (fig. 114 I) by means of relatively thin, single or double mucilage-threads (*m*) which are attached near the sinus; the mucilage-threads are secreted through special pores (fig. 114 G, H). The highly specialised *Oocardium* (156), found in calcareous waters, occurs as hemispherical crusts, often covering Mosses, which may be as much as 5 cm. in thickness. These are composed of a number of more or less parallel, dichotomously forked, elongate and hollow tubes consisting of carbonate of lime and occupied by mucilage (fig. 114 L). Each tube widens towards the surface of the colony and at its free end encloses a single slightly constricted cell, much broader than long and with the longitudinal axis at right angles to the axis of the tube (fig. 114 J, K); the cells are unequally depressed on the two sides so that there are only two planes of symmetry. Each individual is thus situated at the end of a cylinder of mucilage (*m*), the envelope of lime (*l*) being precipitated from the water as the result of the assimilatory activity of the cell. The latter secretes mucilage below in the same measure as the lime-envelope lengthens, so that it always lies at the aperture of the tube. Considerable calcareous deposits may be formed by this Desmid (175 *a*).

The colonial Desmids are probably a specialised development of the ordinary unicellular habit and may perhaps represent a parallel tendency with respect to the latter as is seen in the Zygnemoideae with respect to the Mesotaenioideae. Should the formation of a single individual from the zygote, which Pothoff (135) has established for *Hyalotheca*, prove to be the rule among the colonial Desmids, this interpretation would be considerably strengthened. The occurrence of physiological anisogamy in *Desmidium cylindricum* (p. 351) also speaks for such a view. Most of the colonial Desmids have semicells of a simple form (cf. fig. 114) and appear to have evolved from the less specialised unicellular types; this point of view is supported also by the frequency of zygospore-formation.

pores (*p*); I, colony. J–L, *Oocardium stratum* Naeg.; J, K, arrangement of cells in lime-cylinders; L, surface-view. *e*, end-view; *l*, lime; *m*, mucilage, *o*, *Oocardium*-cell; *r*, replication of wall; *s*, side-view. (D after De Bary; G, H, K after Lütkemüller; I after Schröder; J, L after Senn; the rest after West.)

OCCURRENCE AND DISTRIBUTION OF DESMIDS

A large number of Desmids are well adapted to a planktonic life, either by the possession of a thin plate-like (*Micrasterias*) or needle-like shape (some species of *Closterium*), by the protrusion of the cell into more or less elongated processes (*Staurastrum*, fig. 106 F, G) or the presence of long spines (*Xanthidium*, *Arthrodesmus*); the often copious mucilage-envelopes will also aid to enlarge the surface, without great increase in weight. A desmid-plankton is specially characteristic of certain of the purer (oligotrophic) types of waters containing relatively scanty nutriment (48, 67, 131, 187). Many Desmids, however, occur amid other Algae in the quiet margins of pools and lakes. West regarded the frequent armour of spines and processes as a means of defence against the attacks of small aquatic animals, especially pointing out that on wet rocks and in other localities where Amoebae, Oligochaetes, etc. are either absent or very scanty, the Desmids present usually possess a comparatively simple outline. This may, however, be due to other causes.

The only area from which Desmids are seemingly practically absent is the Antarctic continent. As knowledge of the geographical distribution of members of this family increases, it is becoming apparent that they are by no means ubiquitous. True, a certain number of species seem to enjoy a practically world-wide distribution There are many, long since described and easily recognisable species, however, which have only been recorded from certain parts of the world and the Wests (185) were among the first to draw attention to what seem to be definite American, Arctic, African, etc. types (cf. also (49)). Since most Desmids so rarely form zygospores, dispersal over any great area is probably slow; the ordinary individuals are very sensitive even to partial drying, and submergence in seawater is equally fatal. Under these circumstances carriage over any wide expanse of sea by birds is out of the question, except for very small species which do not present any great surface or for the rarely formed zygospores. Dispersal has probably mainly been effected over land-surfaces by slow steps from one piece of water to another, and it is therefore possible that a sound knowledge of the distribution of Desmids would shed considerable light on the question of the land-connections existing in recent epochs of the earth's history.

There is no doubt that some Desmids can withstand considerable desiccation, for example those that occur among Mosses on rocks (68), but the bulk of these are small forms (many of them Mesotaenioideae) that present no large surface. An analysis of the Desmids in Bohlin's list of Algae from the Azores ((13) p. 24) also shows that the forms involved are small or are such as readily form zygospores.

Within limited areas the distribution of Desmids seems largely conditioned by ecological factors. They thrive best in soft water and they are usually most numerous in peaty water which has a trace of acidity. In cultures a neutral or slightly alkaline reaction has been found most suitable and, with rare exceptions (*Closterium moniliferum*), they do not appear to be able to thrive with organic nutriment (1, 137, 176). Except for a few species (e.g. *Cosmarium dovrense*, *Oocardium stratum*) they do not flourish in water containing carbonate of lime in solution (cf. however (62), (137)), although the element calcium is essential for their growth (176). A further consideration of these matters is outside the scope of this book.

INTERRELATIONSHIPS AND AFFINITIES OF THE CONJUGALES

There still remains the question of the relation of the two series of Conjugales that have been distinguished in the preceding pages. The primitiveness of the Mesotaenioideae is clear, not only in their relatively simple chloroplasts and wall-structure, but also in the apparently normal production of four individuals from the zygote. The fact that some Mesotaenioideae produce only two, whilst Demidioideae may occasionally form four, does not in any way detract from the obvious primitiveness in this respect of the former. But with our present knowledge it is impossible to link up the Desmidioideae, with their complex wall-structure, with the other forms, although analogies are perhaps to be found in the membrane-structure of some Zygnemoideae ((163); also (139) p. 341). For the time being, however, it will be well to bear in mind the possibility of a separate origin of Euconjugatae and Desmidioideae.

Many authorities have sharply separated the Conjugales from the other Green Algae (12, 125, 189), but for this there is no warrant. They do not show more outstanding peculiarities than the Oedogoniales or Siphonales, and the absence of motile reproductive stages, on which much stress has been laid, is a feature which occurs widely in the Chlorococcales. On the other hand in their metabolism they agree altogether with other Green Algae (57, 130).

Their most marked characteristic is no doubt the process of conjugation, but fusion of amoeboid gametes is not uncommon in other Green Algae, being found for example in species of *Chlamydomonas* and in various Chaetophoraceae (p. 257). In those species of the former in which the gametes are covered with a membrane and in which the latter is not discarded prior to sexual fusion, a kind of canal is formed linking up the two cells (cf. fig. 25 K, L, p. 112). The conjugation of *C. eugametos*, as described by Moewus ((119a) p. 471), is particularly significant in this connection (fig. 111 F–H). Such cases show much resemblance to the process of sexual fusion in one of the Mesotaeniaceae or even in one of the Zygnemaceae ((12) p. 168).

In the light of these facts there does not appear to be much difficulty in visualising the origin of the process of conjugation. Perhaps a greater difficulty in deriving the Conjugales from a simple chlamydomonadine origin is to be found in the undoubted primitively axile chloroplasts of the former class.

Schussnig (155) has suggested a derivation of Conjugales from the line of evolution of the Chlorococcales which likewise show a tendency to the suppression of motility. This view is based on the concept that the nucleus of Conjugales is a compound structure and presumes that the ancestral forms were multinucleate. The conjugating cells are regarded as gametangia which have become uninucleate. There does not appear to be any adequate evidence in favour of this hypothesis.

Earlier views that related the Conjugales to the Bacillariophyceae (Diatoms), with which there is considerable superficial similarity, and to the Dinophyceae (Peridinieae), for which there was really never any valid reason, are only of historical interest and need not be discussed here.

The following is a synopsis of the classification adopted in the preceding account:

Suborder I: Euconjugatae:

(*a*) *Mesotaenioideae:*

1. *Mesotaeniaceae:* Ancylonema, Cylindrocystis, Mesotaenium, Netrium, Roya, Spirotaenia.

(*b*) *Zygnemoideae:*

2. *Zygnemaceae:* Debarya, Spirogyra, Zygnema.
3. *Mougeotiaceae:* Mougeotia, Sirogonium, Temnogametum, Temnogyra, Zygogonium.
4. *Gonatozygaceae:* Genicularia, Gonatozygon.

Suborder II: Desmidioideae:

5. *Desmidiaceae:*
   - (i) *Penieae:* Penium.
   - (ii) *Closterieae:* Closterium.
   - (iii) *Cosmarieae:* Arthrodesmus, Cosmarium, Cosmocladium, Desmidium, Docidium, Euastrum, Gymnozyga, Hyalotheca, Micrasterias, Onychonema, Oocardium, Pleurotaenium, Sphaerozosma, Spondylosium, Staurastrum, Xanthidium.

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Order VIII. *SIPHONALES*

The outstanding feature of the Siphonales is the rare production of septa, the variously branched filaments of which the thallus is commonly composed affording the most typical examples of coenocytic construction to be found among the Algae. The structure of these filaments is, generally speaking, of a uniform plan throughout the group. The cytoplasm forms a moderately thick lining layer beneath the wall and bounds a continuous central vacuole occupied by sap; where special mechanical devices are absent, as for instance in the common *Vaucheria*, the threads consequently collapse as soon as the protoplasm is killed and turgor no longer comes into play. Within the lining cytoplasm are situated many discoid chloroplasts, commonly possessing pyrenoids, whilst internal to them are found numerous small nuclei (10). In the growing apices chloroplasts and nuclei often show an inverse arrangement ((12) p. 267, (65)).

The vast majority of the Siphonales inhabit the sea, more especially in the warmer regions of the earth, and the only freshwater representatives are furnished by some of the Protosiphonaceae and the Vaucheriaceae, the latter combining a simple vegetative construction with the most advanced reproductive mechanism. The vigorous development of the order in a marine environment is exemplified by *Bryopsis* (fig. 117) and *Caulerpa* (fig. 118), in which the coenocyte attains to marked morphological complexity, the elaborately organised Dasycladaceae with a plant-body built up by dense aggregation of whorled branches (fig. 123 et seq.), and the Codiaceae with a compact thallus composed of closely apposed and intertwined coenocytic threads (fig. 133). The last two families show a great degree of parallelism with the dominant types of construction in many Phaeophyceae and Rhodophyceae (cf. p. 23). Many of the Siphonales are abundantly encrusted with carbonate of lime and play a part in the formation of marine calcareous deposits, a rôle which they have evidently fulfilled since remote geological ages, as a considerable number of fossil species and genera are known from the earliest times onwards (cf. p. 397). All the forms so far mentioned develop septa in the main only in connection with reproduction, but there is a big series of Siphonales, the Valoniaceae, in which a peculiar septation into multinucleate cells is the rule and many of whose members show striking resemblances to some of the Cladophorales.

A coenocytic tendency is well marked among some of the zoosporic Chlorococcales, where the mature cells are often multinucleate prior to reproduction (cf. p. 145). This tendency may well have led to the evolution of a form like *Protosiphon* (fig. 115 A) which some class with Chlorococcales (146, 158) and some with Siphonales (14, 217), and which readily serves as a prototype for the remaining Siphonales. Most authorities assume some such origin from Chlorococcales, although Oltmanns ((146) p. 429) has suggested a possible reduction from forms like Cladophorales. There is, however, little that speaks for reduction among the Siphonales. The obvious differences from Cladophorales are discussed on p. 242.

(*a*) THE FAMILY PROTOSIPHONACEAE

The best known member of this family is *Protosiphon botryoides* (Kütz.) Klebs ((16 *a*), (108), (124 *a*) p. 499), which commonly frequents the damp mud round the edges of ponds and other similar situations. A slightly different form has proved to be abundant on the desert silt in Egypt (71, 136 *b*). *Protosiphon* is usually intermingled with *Botrydium granulatum* (p. 495) with which, prior to Klebs' investigations, it was confused (166). The coenocyte is normally differentiated into a green spherical or tubular aerial portion and a colourless rarely branched subterranean rhizoid which may reach a length of 1 mm. (fig. 115 A). Such forms show considerable resemblances to *Codiolum* (p. 154) which, however, is uninucleate. Both parts of the *Protosiphon*-plant are occupied by a continuous vacuole, the parietal cytoplasm beneath the thin cellulose wall harbouring numerous nuclei and, in the aerial portion, a reticulate chloroplast with a number of pyrenoids (fig. 115 E, *c*).

Protosiphon does not, however, always appear in this well-defined form. Iyengar (100) records it as commonly growing on walls in India where the individuals, on the upper and drier parts, show a progressive abbreviation of the rhizoid until forms are obtained which are scarcely to be distinguished from a *Chlorococcum*-cell. In cultures Klebs also observed branched thread-like growths.

The young spherical individuals can multiply by successive division of the contents into 4–16 rounded parts which, after acquiring membranes of their own, grow into new plants, a method of reproduction altogether like that of many Chlorococcales. Fully grown individuals frequently exhibit lateral budding of the aerial portion (fig. 115 E); the buds subsequently become cut off by a wall and form new plants, although they may often cohere for a time and may even in this way give rise to short septate filamentous growths.

When plants of *Protosiphon* are submerged the protoplast divides to form a considerable number of biflagellate uninucleate swarmers (fig. 115 F), which are liberated through an apical opening. The swarmers (fig. 115 J) usually behave as gametes and sometimes show some differences in size; gametes from the same parent-individual may copulate with one another (124 *a*). The quadriflagellate zygote soon forms a thick-walled lobed resting spore (fig. 115 B). In the absence of fusion thin-walled parthenospores (fig. 115 C) are produced which can germinate direct or may at an early stage form further swarmers (fig. 115 D). The individuals arising from parthenospores remain spherical for a considerable time, gradually enlarging and becoming multinucleate (cf. fig. 115 I).

As a result of desiccation or exposure to strong insolation the cytoplasm becomes broken up by centripetal furrows into a number of

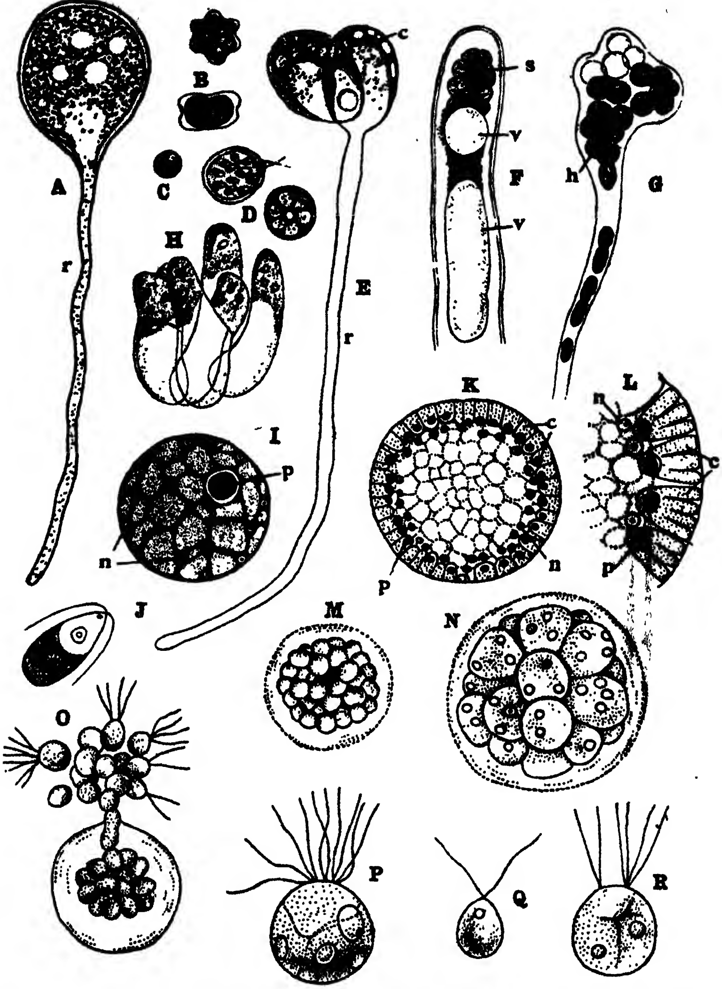

Fig. 115. A–J, *Protosiphon botryoides* (Kütz.) Klebs; A, a normal plant; B, zygotes; C, parthenospore; D, formation and liberation of swarmers from same; E, budding; F, apex of a plant commencing to form swarmers; G, cyst-formation (cysts partly emptied); H, group of plants grown in a nutrient solution; I, young cell formed from swarmer; J, swarmer. K–R, *Follicularia paradoxalis* Miller; K, section of mature cell; L, edge of same enlarged; M, swarmer-formation; N, formation of large spores; O, swarmer-liberation; P–R, diverse swarmers from the same mother-cell. *c*, chloroplast; *h*, hypnospore (cyst); *n*, nucleus; *p*, pyrenoid; *r*, rhizoid; *s*, swarmer; *v*, vacuole. (A–D, F, H after Klebs; E, G after Rostafinski & Woronin; I, J after Moewus; the rest after Miller from Printz.)

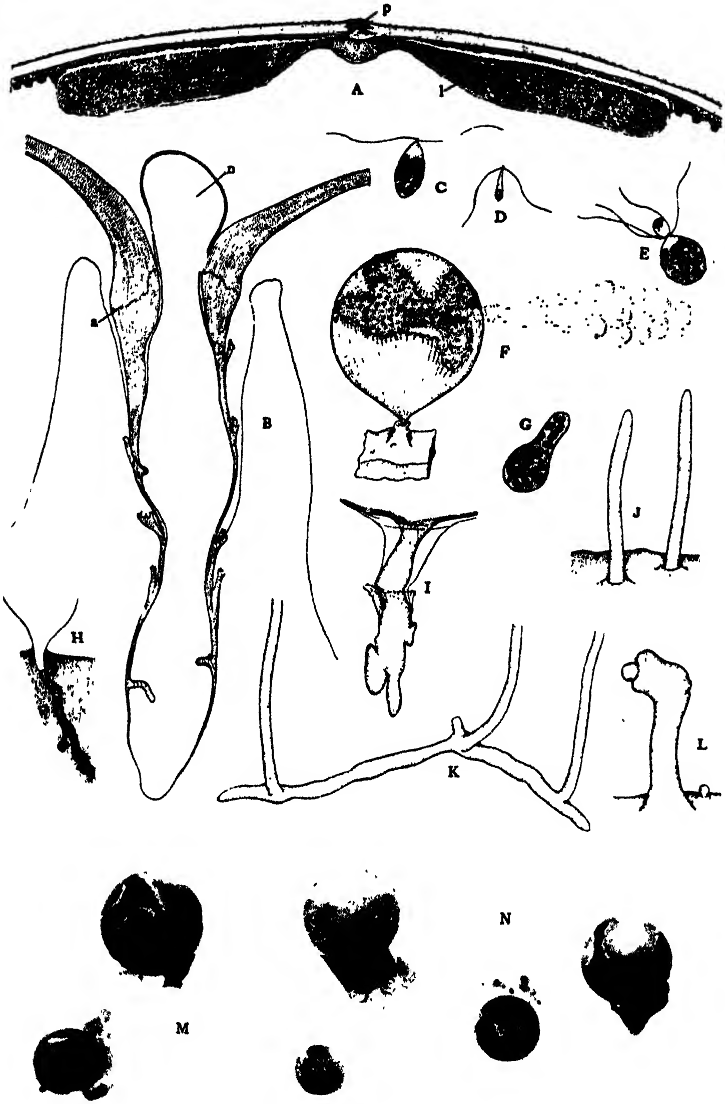

Fig. 116. Structure and reproduction of *Halicystis ovalis* (Lyngb.) Aresch. (H after Kuckuck, the rest from original drawings and photographs kindly supplied by Mr G. J. Hollenberg). A, section through nearly mature reproductive

hypnospores, often with a thick membrane and red-coloured contents (fig. 115 G). These either grow into a new individual direct or give rise to swarmers. *Protosiphon* is probably haploid (124 *a*).

Halicystis (15, 113, 134)[1] is represented by two species in the Atlantic and Pacific oceans, growing at or below the level of the lowest tides. The plant consists of an oval or spherical vesicle, as much as 3 cm. in diameter (fig. 116 M, N), continued below as a slender rhizome (fig. 116 B, H, I) which may be somewhat branched or tuberous, and which is deeply embedded in the calcified crusts of the red alga *Lithothamnion*. In the marginal cytoplasm of the vesicle the nuclei are peripheral and the numerous chloroplasts form a layer adjacent to the large central vacuole. The protoplasm in the rhizome of older plants is arranged in longitudinal folds which nearly obliterate the central vacuole. Similar, but lower folds appear in the vesicle prior to and during the formation of reproductive areas.

Swarmer-formation is initiated by an accumulation of cytoplasm in localised areas which are usually towards the apex of the vesicle. These fertile regions are cut off from the vegetative portion by a thin cytoplasmic layer only (fig. 116 A, *l*). Kuckuck (113) records numerous biflagellate swarmers of two kinds produced from separate plants (fig. 116 C, D). Hollenberg (cf. also (188)) informs me that there is a forceful discharge of swarmers (cf. fig. 116 F) through one or more pores (fig. 116 A, *p*) which develop in the wall. Cytoplasm migrates into the region thus rendered nearly empty, after which successive crops of swarmers may be produced at regular, bi-weekly intervals which are correlated with the tides. Hollenberg finds that the swarmers are macro- and microgametes, having observed their fusion (fig. 116 E) and the germination of the zygotes (fig. 116 G).

A filamentous branching protonemal structure (fig. 116 K) results which may grow over the substratum for some distance but, after

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[1] I am indebted to Mr G. J. Hollenberg of Stanford University, California, U.S.A., for all except H in fig. 116, as well as for the following account. Mr Hollenberg's work is in course of publication in the *American Journal of Botany*.

area with the limiting cytoplasmic layers (*l*); B, longitudinal section of a mature rhizome showing basal thickening of the wall of the vesicle, the line of abscission (*a*), and the origin of a new vesicle (*n*) by the formation of a cross-wall; C, female and D, male gametes; E, sexual fusion; F, diagram to illustrate the forceful discharge of the gametes; G, germling three days after fertilisation; H, perennating rhizome; I, rhizome dissected out of *Lithothamnion*; J, plants, one year old; K, branching protonemal growth of germling; L, pinnacle-like growth of *Lithothamnion* which often forms around the base of the plant enclosing the rhizome, the vesicle being borne at the apex of the pinnacle; M, N, plants with mature reproductive areas and pores, those with the darker areas are females (enlarged about four times). *p*, pore of dehiscence.

rhizomes have been formed by penetration of the *Lithothamnion*, is finally represented by a short erect filament only (fig. 116 J). Growth of the plant is very slow, the small vesicles first produced being almost flush with the surface. Successively larger vesicles develop as the rhizome becomes well established. Towards the end of the growing season the vesicular portion of the plant is often shed, becoming detached at a line of abscission (fig. 116 B, *a*) which is previously formed. This may be preceded by the development of a new vesicle (fig. 116 B, *n*), arising by the formation of a curved cross-wall between the rhizome and the old vesicle. Such a process of regeneration may take place for a number of successive seasons (cf. *Acetabularia*, p. 395).

Another striking member of this family is *Follicularia* (123), at present only known from freshwater in Central Russia, in which the spherical coenocytes (fig. 115 K) are free-floating. They occur either singly attached to one side of a wide gelatinous envelope formed by periodic gelatinisation of the outermost layer of the wall, or as colonies of 6–32 small cells of unequal size enclosed in a common envelope; several envelopes may be present, one within the other. The parietal cytoplasm includes numerous densely apposed, more or less prismatic chloroplasts, each with one pyrenoid, and internal to them numerous small nuclei (fig. 115 K, L).

Reproduction is effected by simultaneous division of the contents into 8–32 multinucleate parts of unequal size (fig. 115 N), which are liberated by gelatinisation of the envelope and grow direct into new individuals. In other cases there is division into more numerous parts (fig. 115 M) which are liberated as swarmers (fig. 115 O), many of which are compound with several nuclei, a number of pyrenoids, and several pairs of apical flagella (fig. 115 P–R). These swarmers are asexual and give rise to new coenocytes after coming to rest. Thick-walled hypnospores may also be formed in place of the swarmers. This peculiar genus is of interest in view of the compound character of its zoospores which show some resemblance to those of *Vaucheria*. Schussnig's *Sphaerosiphon* (176), an epiphyte on marine Algae, possesses a very similar structure, the only method of reproduction known being by means of aplanospores.

Printz (158) refers *Halicystis* to the Valoniaceae, but it appears more nearly allied to the forms just considered, all of which as a matter of fact serve to connect the Chlorococcales with the Valoniaceae.

(*b*) THE FAMILY CAULERPACEAE

There appear to be no good reasons for referring *Bryopsis* and *Caulerpa* to distinct families as is usually done, since the simpler forms of the latter do not differ in any essential respects from the former. Both exhibit a pronounced morphological elaboration of the coenocyte, without any tendency towards the pseudoparenchymatous construction that characterises Codiaceae and Dasycladaceae.

Bryopsis. The genus *Bryopsis*, with its delicate bi- or tri-pinnate fronds, is most abundantly represented in warmer seas, only *B. plumosa* (Huds.) Ag. ((87) pl. 3) (fig. 117 A) and *B. hypnoides* Lamx. ((87) pl. 119) being found in spring or early summer on British coasts, usually near or below low-water level. The plants consist of an inconspicuous, creeping, filamentous and little branched rhizome (25) anchored by rhizoids and giving rise on its upper side to relatively thick vertical threads which are usually naked below, but higher up bear more or less pinnately disposed laterals (fig. 117 M). These themselves exhibit a dense and regular pinnate branching (fig. 117 B), commonly in one plane, the pinnae being formed in acropetal succession and mostly decreasing regularly in length from the base to the apex; this latter feature is especially marked in *B. plumosa* (fig. 117 A). In *B. corticulans* Setchell (187) rhizoidal outgrowths emerge from the bases of the pinnae and form a cortical investment over the axis (fig. 117 C, *r*).

There is a distinct constriction at the point of origin of each pinna (fig. 117 F), and here the otherwise rather thin membrane, which is composed of callose and pectic substances with traces of cellulose (124), shows a slight degree of internal thickening. No true septa are, however, formed prior to the reproductive period, and the entire *Bryopsis* plant contains one continuous vacuole lined by the cytoplasm containing the numerous nuclei and chloroplasts, some of which are commonly devoid of pyrenoids (66). The cytoplasm often shows streaming movements (141, 159). Skeletal strands, considered more fully under *Caulerpa*, are stated to be found extending into the central cavity in a few species ((158) p. 300). The sap contains spherical protein masses (11, 117, 143) which collect at points of wounding and help in the formation of a new membrane (82).

It is probable that the rhizome serves as a means of perennation, although it is doubtful whether this occurs in northern waters. During the growing season creeping threads can arise from the bases of the upright branches and in their turn give rise to new erect systems, so that the growth is generally tufted. Vegetative multiplication readily takes place by detachment of pinnae which become plugged at the point of abstriction and may develop basal rhizoids before detachment (168). The only other method of reproduction is sexual, the pinnae from below upwards becoming converted into gametangia producing two kinds of gametes, usually on distinct plants.[1] Freund (70) has recorded various irregularities.

The preliminary step in the formation of a gametangium is the development of a septum cutting off the pinna from its main axis

[1] See (12) p. 362, (46) p. 37, (156), (199) p. 66, (203) p. 217.

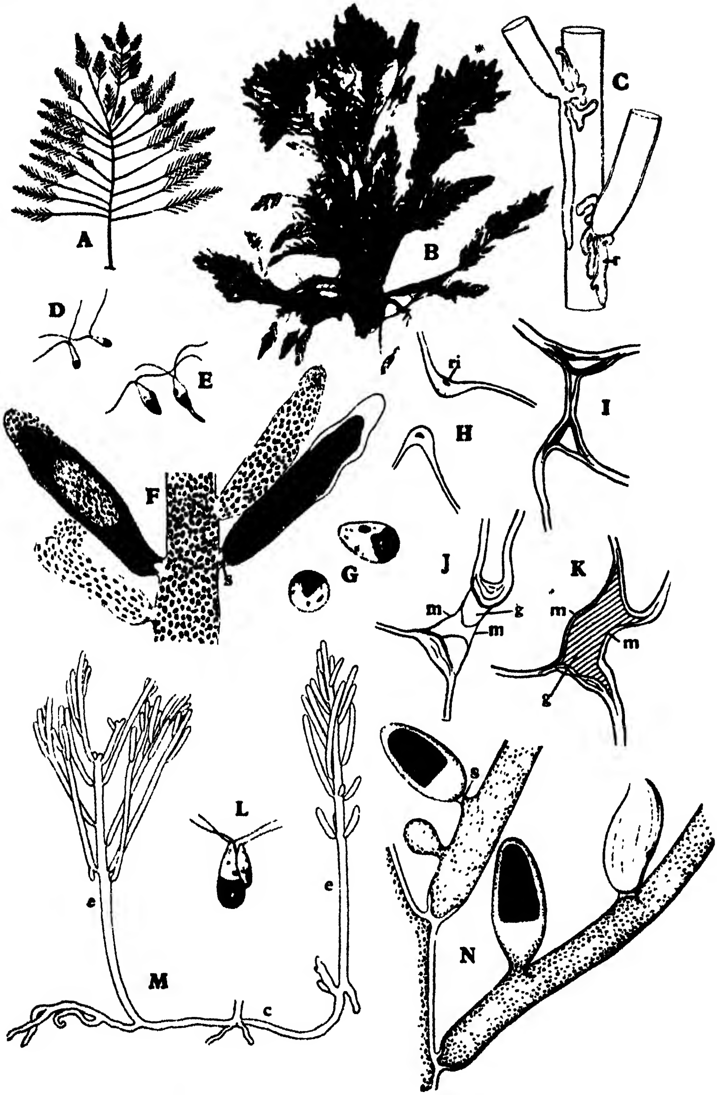

Fig. 117. Structure and reproduction of *Bryopsis*. A, D–F, H–K, *B. plumosa* (Huds.) Ag.; A, habit; D, male and E, female gametes; F, part of a plant with female gametangia; H, J, K, normal sequence of septum-formation at base of a gametangium; I, abnormal case where the closure of the septum is not accompanied by marked gelatinisation of the first-formed wall. B, C,

(fig. 117 F, *s*), although occasionally such septa are lacking and the production of gametes then takes place also in the main axis. The septa (124) arise by the formation of a ring-shaped thickening (fig. 117 H, *ri*) around the constricted base of the pinna, the layers of thickening gradually swelling so as to leave only a narrow cytoplasmic connection between the pinna and its axis. Subsequently this strand of cytoplasm is ruptured and two membranes (*m*) arise on either side of the original thickening (*g*) which usually gelatinises to form an intervening structureless mass (fig. 117 J, K).

The protoplasmic contents of the gametangia increase and the chloroplasts multiply by division, the pyrenoids gradually disappearing in those of the male gametangia. Later the contents assume a reticulate arrangement, and this is followed by simultaneous formation of the gametes which are liberated by gelatinisation of the apex of the pinna. The gametes are pear-shaped with two apical flagella, the female (fig. 117 E) about three times as large as the male (fig. 117 D) and provided with a prominent chloroplast with a pyrenoid by contrast to the small yellowish plastid of the male. The zygote soon assumes a rounded form and germinates direct to form a new plant. Schussnig (182), without giving details, states that reduction occurs during gametogenesis (cf. *Codium*).

The Mediterranean *Pseudobryopsis* ((27), (146) p. 403), with the same habit as *Bryopsis*, is distinguished by the presence of septa at the bases of the pinnae even in the vegetative condition, and more particularly by the development of special oval or pear-shaped gametangia arising as lateral outgrowths from the basal parts of the lower pinnae and cut off in the usual way by a septum (fig. 117 N). In the development of special gametangia this genus exhibits a higher differentiation than *Bryopsis* and approaches the Codiaceae.

Bryopsis has frequently been used for polarity experiments, since inversion is readily obtained (cf. (141), (144), (194), (224)). In dull light the apices of the main axes and of the pinnae easily grow out into rhizoids and, if a thallus is planted upside down, the same phenomenon is observed.

Caulerpa. The majority of the species of *Caulerpa* attain to a far higher morphological differentiation.[1] They are most widely represented in the Tropics, although the classical *C. prolifera* (Forsk.) Lamx.

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[1] See (19), (22), (24), (25), (131), (165), (201), (214).

B. corticulans Setchell; B, habit; C, rhizoid-formation from bases of laterals. G, L, N, *Pseudobryopsis myura* (J. Ag.) Berth.; G, zygotes; L, sexual fusion; N, part of plant with gametangia. M, *Bryopsis corymbosa* J. Ag., habit. *c*, rhizome; *e*, upright shoots; *g*, gelatinised matter of septum; *m*, membranes apposed to latter; *r*, rhizoid; *ri*, ring of thickening initiating septum; *s*, septum. (A, C after Setchell & Gardner; B original; D–F after Pringsheim; G, L, N after Berthold from Oltmanns; H–K after Mirande; M after Boergesen.)

(fig. 118 I) occurs abundantly in the Mediterranean (163), where in recent years a second smaller species (*C. Ollivieri*) has been found by Dostal (57). Species of *Caulerpa* often cover extensive tracts of the sea-floor, mostly in relatively shallow and moderately quiet waters (e.g. of lagoons protected by coral-reefs), and several of them (e.g. *C. prolifera*, *C. crassifolia*) are of interest as being among the few marine Algae which are not lithophytes, their long creeping rhizomes being "rooted" in sand or mud; a large number, however, grow attached to rocks, dead corals, etc., and some of these can thrive in localities exposed to a certain amount of wave-action. A supposed fossil species described by Murray (132) is probably of an altogether different nature.

The general plan of construction is much the same in all cases (fig. 118). A prostrate more or less branched cylindrical rhizome, which in the forms inhabiting sand may be as much as a metre in length, bears numerous well-branched anchoring rhizoids (*r*) below and a number of upright assimilatory shoots, sometimes reaching a length of 30 cm. on its upper side. In *Caulerpa fastigiata* (fig. 118 A) the upright shoots consist of irregularly branched threads like those composing the rhizome, and such a form is but little removed from *Bryopsis* or one of the simpler Codiaceae. In a large number of species the rhizome bears upright cylindrical axes upon which are borne lateral outgrowths (assimilators) which are commonly flattened; their form and arrangement, however, varies greatly, so that the upright axes simulate to a remarkable degree the habits of the shoots of diverse higher plants. Thus, in *C. verticillata* (fig. 118 B) these "leaves" are cylindrical and whorled giving the habit of a *Chara*; in *C. Selago* (Turn.) Ag. they are long, subulate, imbricate structures densely covering the upright axes; while in *C. hypnoides* (R. Br.) Ag. the habit is moss-like. Among the most striking forms are *C. macrodisca* Decne. and *C. Chemnitzia* (fig. 118 D), the appendages of the former resembling the leaves of a Pennywort. Similar leafy outgrowths sometimes occur as "scales" on the rhizomes.

By contrast to these forms with more or less radially organised erect axes are a considerable number in which the latter are bilateral. Thus, in *C. taxifolia* (fig. 118 C) the laterals are arranged in two rows, so that the upright axes recall the shoots of a Yew. In other species the erect axes appear as flat, leaf-like, shortly stalked assimilators arising directly and commonly in two rows from the rhizome. In *C. crassifolia* Ag. and *C. scalpelliformis* (fig. 119 A) they are pinnately branched, but in *C. prolifera* (fig. 118 I) they are entire broad leafy structures, commonly (especially in exposed localities) producing secondary assimilators on their surface.[1]

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[1] With respect to the conditions of their formation, see (183).

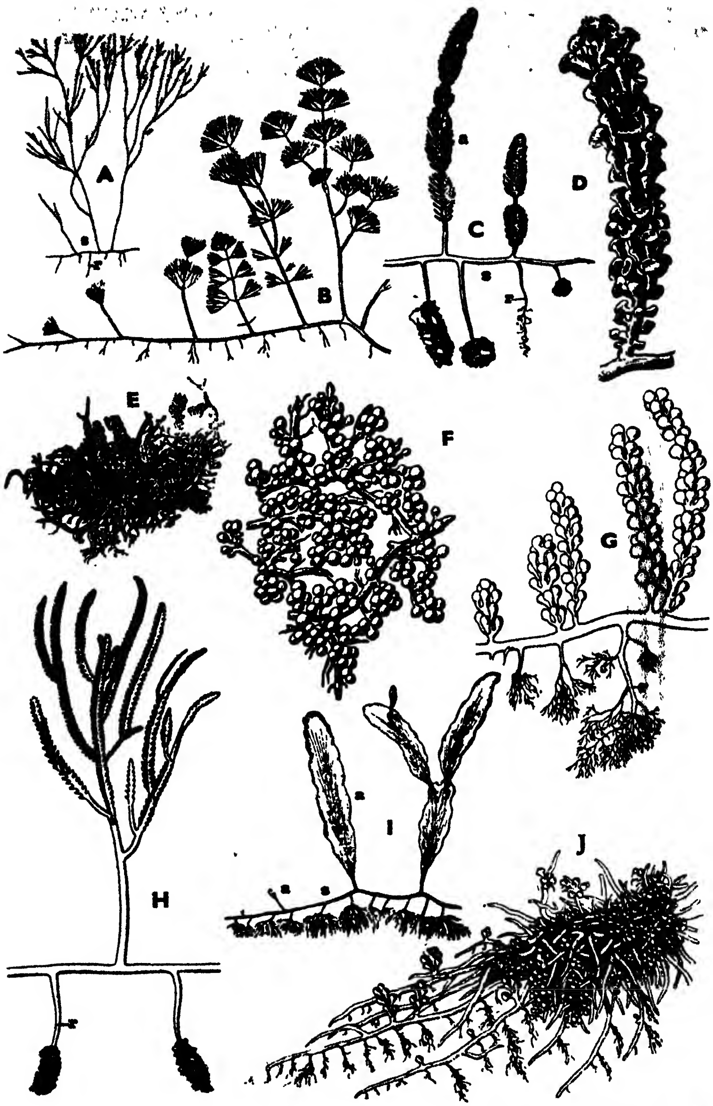

Fig. 118. Habit of *Caulerpa*. A, *C. fastigiata* Mont. B, *C. verticillata* J. Ag. C, *C. taxifolia* (Vahl) Ag. D, *C. Chemnitzia* (Esp.) Lamx. E, *C. laetevirens* Mont. forma *caespitosa*. F, *C. clavifera* (Turn.) C. Ag. G, *C. racemosa* (Forsk.) van Bosse var. *uvifera* (Turn.) van Bosse. H, *C. cupressoides* (Vahl) Ag. I, *C. prolifera* (Forsk.) Lamx. J, *C. racemosa* var. *clavifera* (Turn.) van Bosse. *a*, assimilator; *r*, rhizoid; *s*, rhizome. (A after Reinke; D, E, F after Svedelius; I after Zimmermann; the rest after Boergesen.)

Both Svedelius (201) and Boergesen (19) regard the radial types as more primitive than the bilateral ones, since the latter are often radial at the base. Moreover, the two types of shoots are not uncommonly found on the same plant and several species are known in which both radial and bilateral forms occur in different habitats (e.g. *C. cupressoides*, fig. 118 H). Svedelius suggests that the bilateral types, with more or less broad leafy erect axes, possess an especially advantageous assimilatory equipment, but are ill suited for growth in disturbed water. Such forms do not in fact occur in exposed localities. According to Boergesen the radial forms are practically restricted to shallow water, whereas the bilateral types occur both there and in deep water where they play the dominant rôle. Some of the more plastic bilateral species show a more and more marked distichous arrangement of the laterals in poorly illuminated situations (muddy or deep water). The Mediterranean *C. prolifera* extends to a depth of 15 metres, while other species have been found down to 50 metres and even lower.

Svedelius and Boergesen (cf. also (17)) have materially contributed to our knowledge of the ecology of the *Caulerpas*. Both distinguish three groups of forms distinctive of different habitats. *C. verticillata* (fig. 118 B), which usually occurs on rocks, collects large quantities of fine mud and organic detritus amidst its felt of thread-like rhizomes; these exhibit an oblique or often an almost vertical growth and are thus able to reach the surface when covered. The second group is constituted by the species inhabiting the sandy or muddy bottom in shallow or deeper water. In many of these the tip of the rhizome is pointed, so that it can bore its way through the substratum. The rhizoids are at first undivided, but at a depth of 2–3 cm. branch richly, so that uprooted plants often bring with them a whole clump of sand fastened together by the branches (cf. fig. 118 C). Boergesen cites *C. cupressoides* (fig. 118 H) as the most characteristic species of this group. In the third group we have the forms inhabiting rocks and coral-reefs, of which one of the most important is *C. racemosa* (fig. 118 G), represented by diverse forms, partly growing in exposed and partly in more sheltered localities. The rhizoids of these rock-inhabiting forms usually divide immediately beyond the point of origin from the rhizome.

Not only is there an immense range of form among the species of the genus, but there is also considerable variability in individual habit. In situations more exposed to the action of waves, several of the plastic rock-inhabiting species exhibit a reduction of the erect axes, which then occur only at relatively wide intervals, and a greater development of the rhizome whose branches become felted together, so that irregular cushion-shaped growths are produced (fig. 118 E, J). The rhizoids in such cases fasten themselves to all the irregularities in the rock and secondary rhizoids commonly develop from the erect axes. Tandy (233) records other instances of plasticity.

Internally the *Caulerpas*, like *Bryopsis*, are characterised by the complete absence of septation, central vacuole and lining cytoplasm with chloroplasts[1] (devoid of pyrenoids) and nuclei being continuous throughout the plant; in *C. hypnoides*, however, a small cell is cut off at the tip of each "leaf". According to Prat (154) the vacuole contains colloids which coagulate in fixatives. The different parts of the thallus grow at their apices, where a dense aggregation of proto-

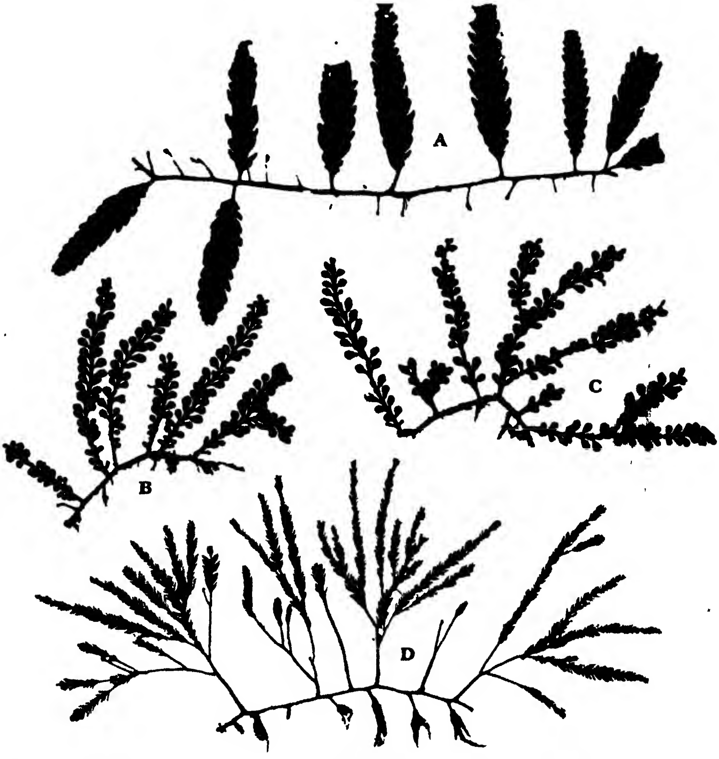

Fig. 119. Habit-photographs of *Caulerpa* (photos by Prof. M. O. P. Iyengar of Madras). A, *C. scalpelliformis* (R. Br.) van Bosse. B, C, *C. Fergusonii* Murr. D, *C. sertularioides* (Gmel.) Howe.

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[1] The distribution of the chloroplasts varies with the illumination; at night, as well as during artificial darkening, they retreat from the apices of the fronds, the movements being due to cytoplasmic currents (58*a*).

plasm is to be found. *Caulerpa* is specially distinguished by the abundant development of more or less cylindrical skeletal strands (48, 101, 136*a*, 139, 200) traversing the central cavity in all parts of the thallus. These are most strongly developed as a rule in the rhizomes, where they form an almost radial system, often knotted together in a prominent manner in the centre (fig. 120 A), whilst in the flat assimilators they run irregularly from surface to surface (fig. 120 B); they are absent or poorly developed in the rhizoids.

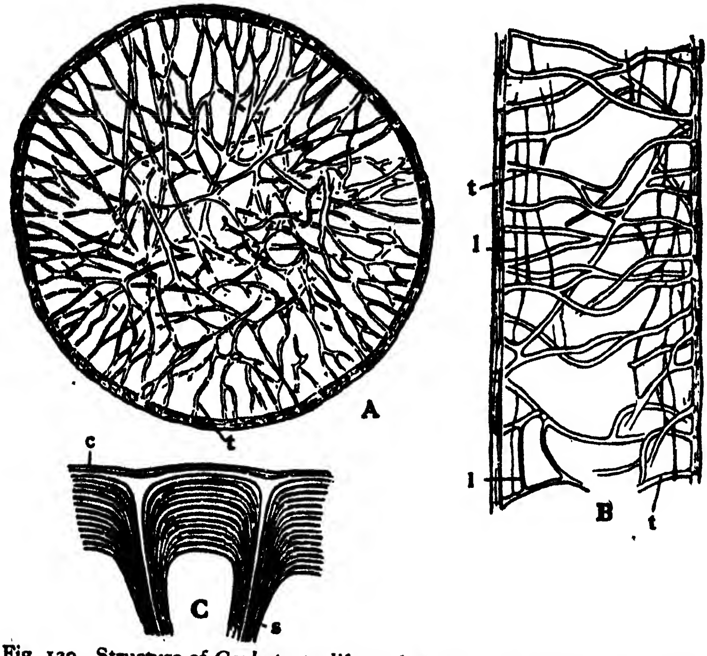

Fig. 120. Structure of *Caulerpa prolifera*. A, section of rhizome, somewhat diagrammatic. B, longitudinal section of assimilator. C, part of the wall with pieces of two skeletal strands. *c*, surface-layer of wall; *l*, longitudinal and *t*, transverse skeletal strands; *s*, first-formed part of skeletal strand. (C after Dippel from Oltmanns; the rest after Oltmanns.)

The strands differentiate from rows of microsomes that appear within clearer areas of the dense apical cytoplasm (101, 200). They are either connected with the membrane *ab initio* or are at first free at one or both ends. Originally thin, like the young membranes (cf. fig. 120 C, *s*), they gradually increase in thickness by the apposition of successive strata which are continuous with those deposited on the longitudinal walls and which lead to the rapid increase of thickness of the latter behind the apex (fig. 120 C). Both the membrane and the skeletal strands, therefore, exhibit a marked stratification due to the different density of the successive layers. Moreover, the axial part of each strand extends through the thickening layers of the longitudinal walls up to the surface strata of the latter, giving a firm connection (fig. 120 C).

The longitudinal walls, as well as the skeletal strands, consist of callose, pectin, pectic acids, and pentose, no cellulose being present (124). At the growing points the strands occur closely crowded, but in the older parts they become rather more widely separated. Although most of the strands run roughly perpendicular to the surface, a certain number follow a longitudinal course (fig. 120 B, *l*) and serve to connect up the others in the longitudinal direction. Every skeletal strand is enveloped on all sides by cytoplasm, but there are also numerous independent cytoplasmic strands traversing the central vacuole and often showing marked streaming (101, 102).[1] Apart from these strands the membrane of diverse species of *Caulerpa* also shows numerous peg-like internal projections (36).

No definite conclusion has yet been reached with respect to the function of the strands. Noll (140) established that solutions of mineral salts diffused more rapidly through the strands than through the cytoplasm and, since the latter is everywhere in contact with them, this feature may be of some significance. The considerable area over which the protoplasm is spread with the help of the strands may well afford some of the advantages in the way of enlargement of surface provided by the numerous walls of a multicellular plant. The strands have also been regarded as mechanical devices to resist turgor pressure due to an occasional high osmotic value of the sap (101), but it is not certainly established that such high pressures are realised and Micheels (122) has even maintained that the osmotic pressure in *C. prolifera* is below that of seawater. The diverse views as to the function of the strands do not necessarily contradict one another.

Up to recent times the only method of reproduction established for *Caulerpa* was vegetative. This takes place abundantly by a gradual dying away of the older parts of the rhizomes, whereby the branches become independent plants; by this means rapid local multiplication is effected. Dispersal is attained by detached fragments which are able rapidly to heal any exposed surface and possess a remarkable power of regenerating new plants when lodged in a suitable position.

In 1928 Dostal (51) reported the discovery in the autumn of the previous year of elongated papillae on the assimilators (cf. fig. 121 A, B) and more rarely on the rhizomes of *C. prolifera*; these he interpreted as possible gametangia in view of the presence of what

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[1] Movement of the cytoplasm under the influence of unfavourable conditions or in relation to reproduction has been studied especially by Dostal (54).

appeared to be swarmers in the abundant mucilage exuding from the apex of some of the papillae. Subsequently he ((52); cf. also (53), (177)) showed that the swarmers are formed within the assimilators and that the papillae only serve for their liberation. Prior to the formation of the papillae the fertile assimilators acquire a variegated appearance, owing to massing of the green contents at certain points, while others become yellow; this paling effect may also show itself in the rhizomes owing to withdrawal of some of their contents. In the green regions the cytoplasm exhibits a reticulate arrangement and it is here that the uninucleate swarmers are formed. They are liberated rapidly through the apices of the papillae in a mass of mucilaginous matter (fig. 121 E) which not only fills the papillae but exudes in large quantities from their tips.

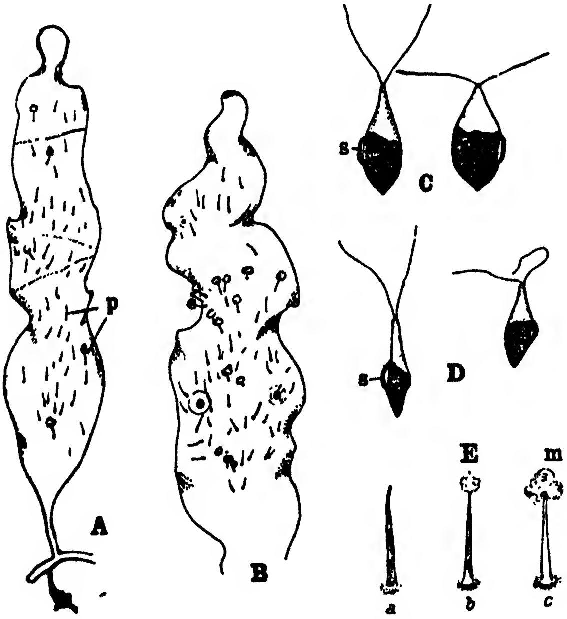

Fig. 121. Reproduction of *Caulerpa prolifera* (after Schussnig). A, B, two fertile assimilators, with papillae through which the swarmers are liberated. C, D, swarmers of two sizes (the difference in size somewhat exaggerated). E, single papillae; *a*, unopened; *b*, *c*, successive stages of gelatinisation; *m*, mucilage; *p*, papilla; *s*, stigma.

These phenomena are not observable only in *C. prolifera*, but have since been met with in *C. Ollivieri* (53, 55) and in material of a number of other species ((4), (58) p. 509, (63)). According to Dostal (53) and Ernst (63) the whole plant in many species disorganises soon after the liberation of the swarmers. As Dostal has pointed out, the process of swarmer-formation in *Caulerpa* shows resemblances to that of *Valonia* (p. 424).

The biflagellate swarmers (fig. 121 C, D) are more or less pear-shaped, but exhibit some change of form, the anterior extremity being sometimes drawn out like a pseudopodium. They possess a single curved chloroplast without a pyrenoid and a prominent elongate stigma. Schussnig (177) and Ernst (63) distinguish two kinds of swarmers (cf. also (100 *a*)), those of *C. prolifera* being of about the same size, but the one (fig. 121 D) narrower than the other and more active in its movements. In *C. clavifera* Ernst describes brownish green sluggish macroswarmers and bright green active microswarmers formed from distinct plants. It is exceedingly probable that the two kinds of swarmers represent gametes, but there is as yet little evidence of their fusion ((100 *a*); cf. (56), (63)). Ernst goes so far as to suggest, however, that the polymorphism of *Caulerpa* may in part be due to hybridisation. Earlier doubts (184) whether the swarmers really belonged to the life-cycle of *Caulerpa* may now probably be dismissed.

According to Haberlandt (81) and Zimmermann (232) plants of *C. prolifera* show marked geotropic irritability, the rhizome being diageotropic, the rhizoids positively and the assimilators negatively geotropic. The curvature takes place some distance behind the apex of the rhizome in a region where Haberlandt finds starch-grains which he believes function as statoliths. If a rhizome is inverted the first rhizoids and assimilators are formed as before on its morphological lower and upper sides respectively, but curve at their tips to respond to the altered geotropic stimulus; after 2–3 days, however, the polarity in the newly grown stretch of rhizome has become inverted and rhizoids and assimilators arise in their customary positions in relation to the orientation of the plant. Detached pieces of assimilators likewise show polarity, rhizoids developing especially from their base and new assimilators from their apex; this is more pronounced in pieces taken from mature assimilators than from young ones. *Caulerpa* has been abundantly used in investigations on polarity and growth-correlation, but further details cannot be included here.[1]

(*c*) THE FAMILY DERBESIACEAE

The rather isolated marine genus *Derbesia* (25, 189), most of whose species favour warmer seas, possesses a creeping irregular rhizome (fig. 122 A, *c*) attached by lobed haptera (*ha*) and bearing dense tufts of upright threads whose degree of branching varies with the species.

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[1] See (49), (50), 102–104), (109), (141), (209).

The upright threads show marked phototropic sensitiveness (11). The structure is typically siphoneous, except that at the base of each branch of the erect system a pair of septa delimiting a small cell are often formed. The central vacuole commonly contains protein-bodies (79, 117, 143) which appear as crystalloids (fig. 122 B), sphaerocrystals,

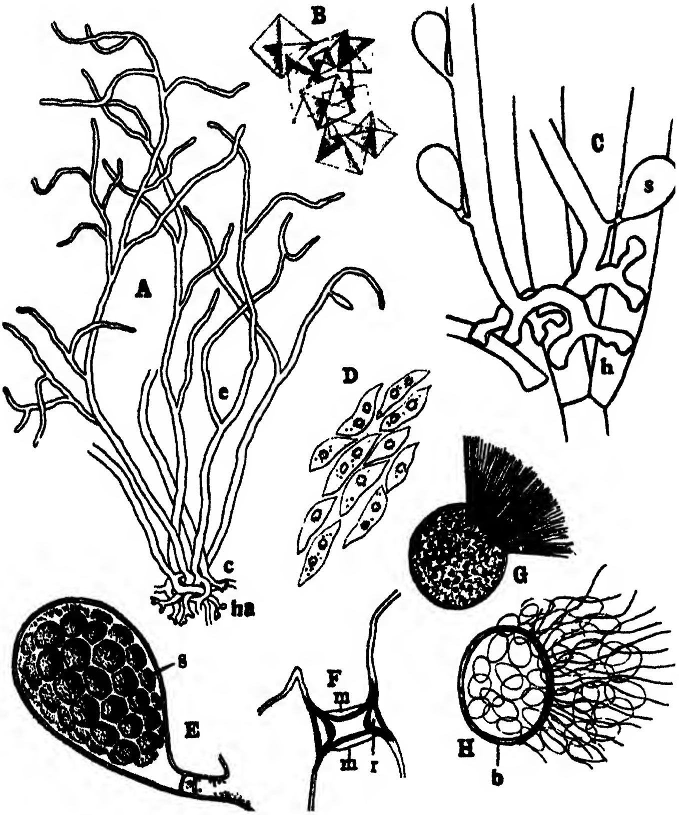

Fig. 122. Structure and reproduction of *Derbesia*. A, *D. neglecta* Berth., habit. B, D, F, *D. Lamourouxi* (J. Ag.) Sol.; B, protein-crystalloids from the cell-sap; D, typical chloroplasts; F, septum-formation. C, *D. tenuissima* (De Not.) Crouan, base of plant growing on *Cladophora* (*h*), with three sporangia. E, G, H, *D. marina* (Lyngb.) Kjellm.; E, zoosporangium; G, zoospore; H, insertion of flagella on the double blepharoplast (*b*). *c*, rhizome; *e*, upright threads; *ha*, hapteron; *m*, membrane of septum; *r*, primary ring of septum; *s*, sporangium or swarmers. (B, D after Ernst; E after Kuckuck; F after Mirande; G, H after Davis; the rest after Boergesen.)

or as fibrous masses, the latter being responsible for the blue-green fluorescence often exhibited by this alga. Ernst (62) has also reported the presence of crystals of calcium oxalate in *D. tenuissima*. The chloroplasts in most species are spindle-shaped with 1–3 pyrenoids (fig. 122 D), but in plants growing in deeper water and less well illuminated they become smaller and discoid and contain no evident pyrenoid.

Reproduction is effected by curious multiflagellate zoospores which are formed in oval sporangia (fig. 122 C) arising as lateral outgrowths from the upright threads. The sporangia are cut off by a complex septum (fig. 122 F) which appears to have the same structure and to be formed in the same way as in *Bryopsis* (cf. p. 377 and (124)). Davis (45) has shown that within the sporangium a large number of the nuclei degenerate, the protoplasm subsequently becoming cleft about the surviving ones (fig. 122 E), so that the resulting 8–20 swarmers are uninucleate. The latter (fig. 122 G) are large and slightly flattened at the anterior end, where there is a ring of flagella arising from a double ring-shaped blepharoplast (fig. 122 H, *b*); they contain a large number of chloroplasts. Their fate is unknown.

In its habit *Derbesia* shows some resemblance to a *Bryopsis*, especially if the sporangia in accordance with several authorities are compared with the pinnae of the latter; other points of agreement are seen in the mode of septum-formation at the base of the sporangium and in the general character of the cell-contents. The zoospores are, however, unique, although in their derivation from a multinucleate protoplast there are analogies with the reproduction of Vaucheriaceae (cf. especially the oogonia). The many flagella perhaps indicate derivation from a compound zoospore like that of *Vaucheria*.

(*d*) THE FAMILY DASYCLADACEAE

The members of this family are characterised, apart from their whorled branching, by the development of specially differentiated reproductive organs and the tendency to a more or less complete incrustation with carbonate of lime. It is this latter feature that is responsible for the preservation of the numerous fossil forms that are known from the Ordovician (Lower Silurian) onwards. According to Pia (149, 153) some sixty fossil genera, by contrast to the ten living ones, have been discovered (cf. p. 397).

The Mediterranean *Dasycladus clavaeformis* (fig. 123 F), which forms dense growths in quiet water of no great depth, appears as the least specialised living member of this family.[1] The unbranched vesicular main axis, which may attain to a length of 5 cm., is anchored

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[1] See (39), (46) p. 44, (142), (146) p. 367.

to the rocky substratum by a richly branched non-septate rhizoid. Except at the very base the central vesicle bears densely aggregated alternating whorls composed of 10–15 members, each of which is branched to the second or third degree (fig. 123 A), the successive segments becoming progressively shorter and narrower, the ultimate ones being pointed; the diverse branches, usually four in number,

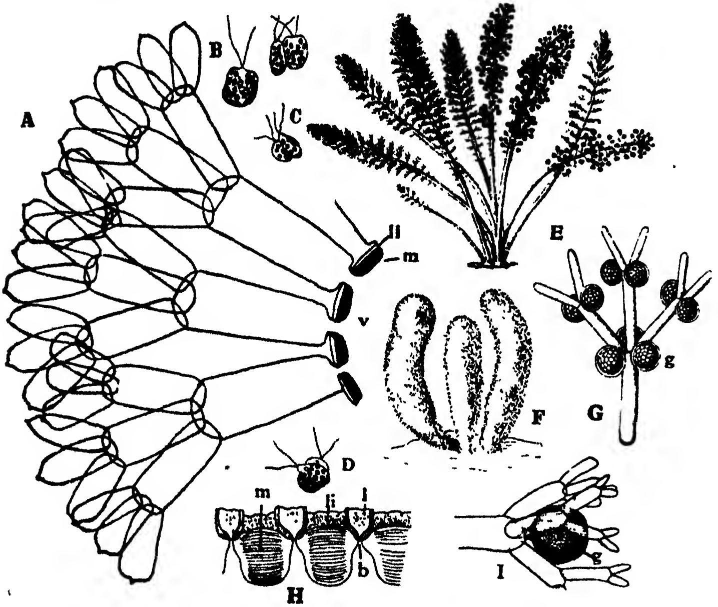

Fig. 123. A–D, F, H, I, *Dasycladus clavaeformis* (Roth) Ag.; A, part of a section of the plant showing the method of branching; B–D, gametes and sexual fusion; F, habit; H, part of wall of central vesicle in section; I, one of the laterals with a gametangium (*g*). E, G, *Batophora Oerstedi* J. Ag.; E, habit; G, one of the laterals with gametangia (*g*). *b*, point of origin of branch; *l*, base of a lateral; *li*, calcified layers of wall; *m*, thickening layers of wall; *v*, central vesicle. (A, F original; E after Boergesen; G after Harvey; the rest after Oltmanns.)

arise from just below the apex of the parent segment. Since all the branches develop to the same length they not only obscure the central vesicle, but form a fairly compact hairy surface (fig. 123 F). The branches are separated from one another and from the main axis by marked constrictions, leaving only a very narrow communication between them (fig. 123 A, H). Between the narrow insertions of the primary branches the wall of the central vesicle is strongly thickened, the thickening showing marked stratification with the outer strata impregnated with carbonate of lime (fig. 123 H). In other words the wall of the vesicle is constituted by a thin cylinder of lime perforated by alternating whorls of narrow apertures, corresponding to the points of insertion of the primary branches. The numerous small chloroplasts, as in all Dasycladaceae, each contain a small pyrenoid. If the apical part of the vesicle is removed by a cut, a new apex is regenerated (67), while if the rhizoidal end is removed and the plant inverted a new apex is formed from the rhizoid-bearing pole (229).

Shortly stalked gametangia (fig. 123 I, *g*) are formed at the apices of the primary branches in the upper half of the plant. They arise as spherical protrusions which receive the bulk of the contents from the adjacent branches before being cut off by a septum. As a result they appear deep green by contrast to the pale colour of the surrounding parts. The details of reproduction are dealt with on p. 401.

A related form is constituted by the West Indian *Batophora Oerstedi* (*Dasycladus occidentalis* Harv.)[1] (21, 24, 93), which is not impregnated with lime and has the whorls of branches much more loosely placed (fig. 123 E). Gametangia, producing a number of globular cysts which give rise to the gametes, are borne laterally in small groups at the ends of the primary and secondary branches (fig. 123 G, *g*).

In *Neomeris*,[2] found on tropical shores and known from the Cretaceous onwards, the structure is more complicated and the calcification in general more profound. The most widely distributed species is *N. annulata* (fig. 124 E), in which each plant consists of a small worm-like calcified mass, 1–2 cm. long and bearing an apical tuft of hairs (not visible in the photograph). As in the preceding forms there is a club-shaped vesicular main axis (fig. 124 A, *a*) attached basally and bearing densely arranged whorls of laterals (30–40 in each whorl) branched to the third degree. The ultimate branches, however, are developed as long delicate hairs which fall off at an early stage and are only recognisable as a characteristic tuft near the apex (fig. 124 A, *h*). There are only two branches of the second order and their apices soon commence to dilate (fig. 124 A, G). Ultimately, as a result of their turgor, these enlarged apices become pressed together and, assuming a six-sided outline, form a compact faceted surface (fig. 124 A, *f*), with the bulk of the chloroplasts apposed to the outer walls. Between the insertions of the primary branches the wall of the main axis is again prominently thickened (fig. 124 F, *m*) and there is only a narrow pore leading into each branch.

Svedelius (202) has shown that a single nucleus passes into each branch and by subsequent division gives rise to the multinucleate condition. In young plants the whorls are more widely separated and

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[1] *Coccocladus occidentalis* of Cramer (39).

[2] See (21), (24), (35), (39), (40), (93), (96), (191).

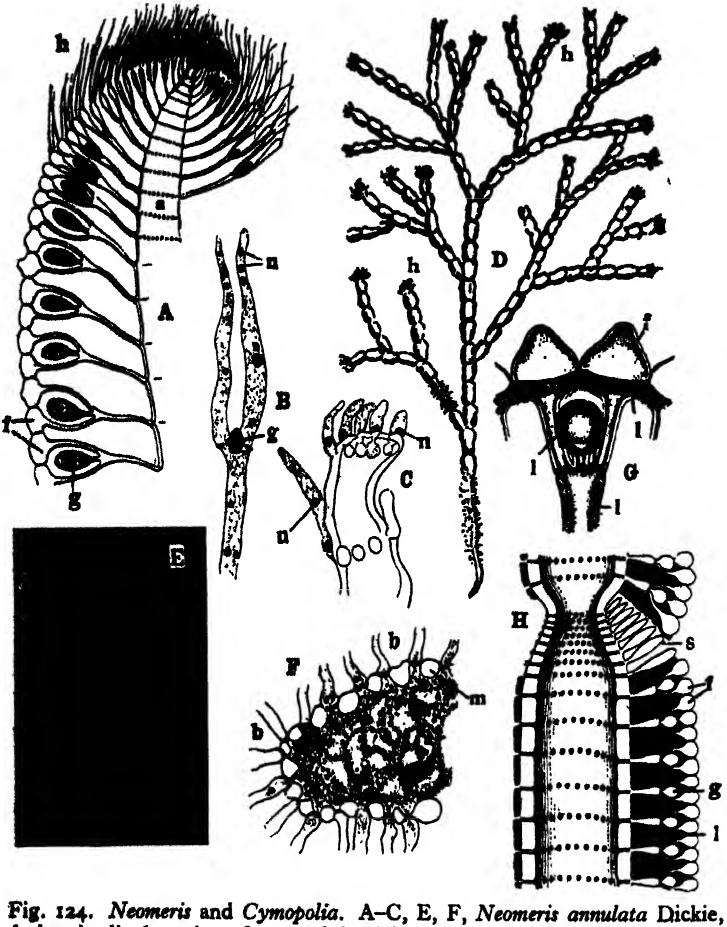

Fig. 124. *Neomeris* and *Cymopolia*. A–C, E, F, *Neomeris annulata* Dickie, A, longitudinal section of apex of decalcified plant; B, primary lateral with uninucleate primordium of gametangium (*g*) arising on one side of the apex; C, longitudinal section of apex of plant; E, habit; F, transverse section of main axis with bases of laterals. D, H, *Cymopolia barbata* (L.) Harv.; D, habit; H, longitudinal section through parts of two segments with an intervening uncalcified joint (*s*). G, *Neomeris dumetosa* Lamx., transverse section. *a*, main axis; *b*, bases of laterals; *f*, facets; *g*, gametangia; *h*, hairs; *l*, lime (shaded); *m*, thickened membrane of main axis; *n*, nucleus; *s*, sterile branches. (A after Cramer; D after Ellis; E, original (photo, R. Cullen); G after Church; H after Solms-Laubach; the rest after Svedelius.)

the general habit is very similar to that of a *Dasycladus* (35). As the arrangement of the whorls becomes more compact, it is at first the ends of the primary branches that become dilated, the change to the mature condition only taking place slowly. The stalked, spherical or oval gametangia (*g*) occupy the same position as in *Dasycladus* when mature (fig. 124 A, G), but according to Svedelius they first arise as lateral outgrowths a little way beneath the apex of the primary branch (fig. 124 B, *g*). The young gametangium contains a single large nucleus which subsequently divides repeatedly. Ultimately the entire contents form a single cyst enveloped by its own membrane in which the part adjacent to the stalk of the gametangium is differentiated as a lid.

Carbonate of lime is deposited (35) as a continuous layer on the inner surfaces of the facets, the resulting cylinder being perforated only by narrow pores traversed by the slender stalks of the secondary branches (cf. fig. 124 G). In addition each primary branch is completely ensheathed in an envelope of lime (*l*) and a similar thick deposit is formed around each gametangium (fig. 124 G). In fact, in some species (e.g. *N. Kelleri*), groups of gametangia are connected by a common ring-shaped mass of lime.

Cymopolia (26, 39, 191), which like *Neomeris* is essentially tropical in its distribution and appears already in the Cretaceous, shows a different outward habit (fig. 124 D). The plants are composed of a series of calcified segments separated by narrower uncalcified joints, the whole arranged to form a thallus subdichotomously branched in one plane and somewhat resembling the red alga *Corallina*. The main axis, attached basally by a richly branched holdfast, shows constrictions at regular intervals (fig. 124 H), and at these points are borne whorls of slightly clavate laterals (*s*), at first bearing tufts of polytomously branched septate hairs which are rich in chloroplasts. No lime is secreted in these regions, but, as a new calcified segment forms above, the hairs fall off and only the primary laterals remain to occupy the narrow joint. The assimilatory hairs are consequently only found at the apices (cf. fig. 124 D). In the region of the calcified segments the axis bears numerous whorls of laterals branched to the second degree, the swollen ends of the secondary branches forming a faceted surface as in *Neomeris*, though less regular in pattern. Gametangia are formed throughout the calcified segments and again appear terminal on the primary branches (fig. 124 H, *g*).

The space between the axis and the faceted surface is at first occupied by mucilage, but later it is filled by a broad continuous cylinder of lime extending from just beyond the periphery of the axis to the inner faces of the facets (fig. 124 H, *l*). This thick cylinder is perforated by canals occupied by the primary and secondary branches and contains spherical cavities in which the gametangia are lodged.

The club-shaped plants of *Bornetella* (1, 2, 40, 191), found only in the southern hemisphere, have much the same habit and structure as *Neomeris*, but there is only a relatively thin cylinder of carbonate of lime (mixed with oxalate of lime) deposited in annular thickenings around the side walls of the facets (fig. 125 A, B, *li*). The most marked peculiarity, however, lies in the fact that the gametangia are borne laterally along the sides of the branches of the first order (fig. 125 A);

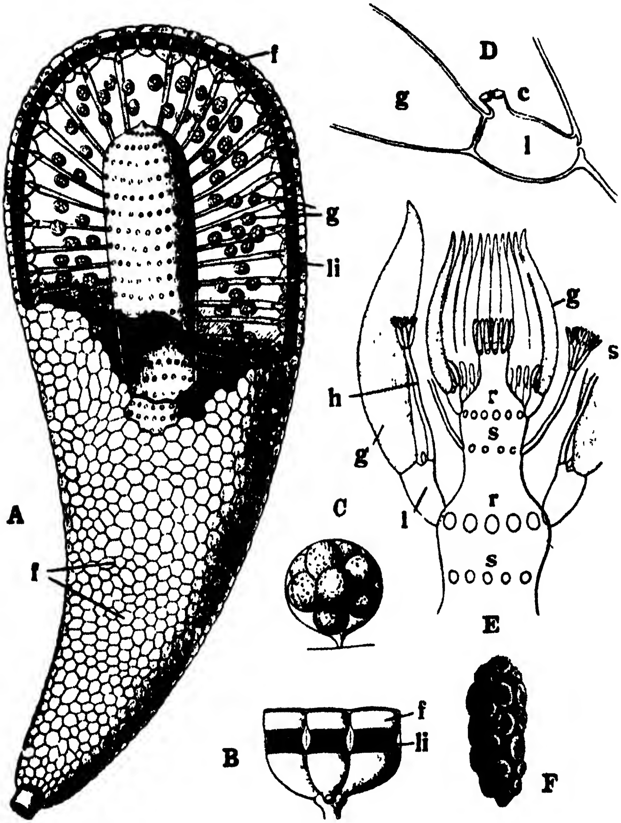

Fig. 125. A, C, *Bornetella oligospora* Solms-Laubach; A, plant, slightly enlarged, cut open above to show the internal structure; C, gametangium with cysts. B, *B. nitida* (Harv.) Munier-Chalmas, end of primary lateral with secondary facets. D, E, *Halicoryne Wrightii* Harv.; D, profile view of fertile whorl; E, upper part of plant with sterile and fertile whorls. F, *H. spicata* Kütz., calcareous spicule with cysts from gametangium. *c*, corona; *f*, facets; *g*, gametangium; *h*, hair; *l*, basal cell of fertile lateral; *li*, lime; *r*, fertile and *s*, sterile whorls. (B, E after Cramer; the rest after Solms-Laubach.)

each produces a number of cysts, part of whose membrane is detachable as a lid (fig. 125 C). In the position of the gametangia and the formation of a number of cysts within them *Bornetella* recalls *Batophora* (p. 389).

On the basis of his observations on *Neomeris*, Svedelius (202) concludes that the forms with lateral gametangia are to be regarded as more primitive, and that the apparent terminal position seen in that genus, as well as in *Cymopolia* and *Dasycladus*, is secondary. He advocates classing the genera so far considered into Dasycladeae with *Dasycladus* and *Batophora* and Neomereae with the three remaining genera, *Batophora* and *Bornetella* being regarded as the most primitive members of their respective groups.

THE ACETABULARIEAE

The Acetabularieae display the most specialised structure among the Dasycladaceae. In the Australian *Halicoryne* (1, 41, 192) the main axes bear alternating whorls of eight sterile and sixteen fertile laterals, the axis being slightly constricted opposite the sterile whorls whose members are hair-like and branched to the third degree (fig. 125, E, *s*). In the fertile laterals (cf. also fig. 125 D) the wide basal cell (*l*) bears a pod-like gametangium (*g*) which is only cut off by a septum at a late stage, and, on the adaxial side, an often reduced hair (fig. 125 D, *c*; E, *h*) resembling one of the sterile laterals. *Halicoryne* can be compared to *Cymopolia*, in which fertile and sterile regions likewise alternate, although there they are not reduced to single whorls. The axis and the gametangia of *Halicoryne* are encrusted with a layer of lime of uneven thickness, but the rest of the plant is uncalcified. The gametangia contain a small number of strongly calcified cysts which form a coherent mass (fig. 125 F).

In the section *Polyphysa* of *Acetabularia* (2, 39, 96, 192) the elongate main axis bears several whorls of repeatedly branched sterile laterals below, and this culminates in the production of a single fertile whorl, although occasionally two such whorls may be formed (fig. 126 B). The fertile members are mainly composed of a long sac-shaped gametangium (*g*), merely separated by a constriction from the basal part of the lateral (*p* representing the primary branch); this bears on its upper side a small protuberance (*corona*) carrying a number of more or less strongly reduced branches (fig. 126 B, *c*). The corona, the basal part of the lateral, and the gametangium are all continuous with one another and with the axis, and such an absence of septa is frequent in the species of *Acetabularia*. In the section *Polyphysa* the gametangia of a whorl are always quite free from one another at first, but in most species of the section they become cemented together subsequently by a deposit of lime. Schussnig (181) has recently described a species of this section from the Mediterranean (fig. 127 B). As in all species of *Acetabularia* the gametangia contain numerous uncalcified cysts.

In the remaining members of the genus the gametangia are more or less completely united organically, apart from being encrusted with lime, and there is both an inferior and a superior corona, the adjacent coronae being free (Sect. *Acetabuloides*) or likewise fused (Sect. *Acetabulum*). The majority of the species of these two sections produce only a single fertile whorl, but in *A.* (*Acetabuloides*) *crenulata* (fig. 126 D, E) sterile and fertile whorls alternate as in *Halicoryne*. The two

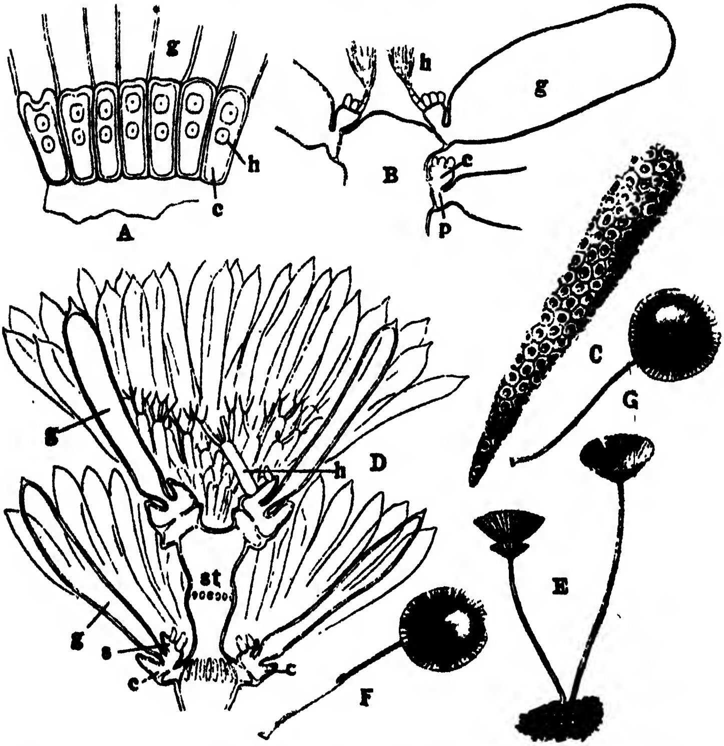

Fig. 126. A, D, E, *Acetabularia crenulata* Lamour.; A, surface view of superior corona (*c*) with pairs of hair-scars (*h*); D, apex of fertile plant in longitudinal section, two fertile whorls separated by scars (*st*) where a sterile whorl was borne; E, habit. B, *A. Moebii* Solms-Laubach, longitudinal section, two superposed fertile whorls. C, *Acicularia Schenckii* Moeb., calcareous spicule with cysts from gametangium. F, G, *Acetabularia mediterranea* Lamx., mature plants, seen respectively from above and below. *c*, corona; *g*, gametangium; *h*, hairs; *p*, base of primary lateral; *s*, superior corona. (E after Boergesen; F, G after Woronin; the rest after Solms-Laubach.)

coronae appear as short outgrowths enclasping the base of each gametangium (fig. 126 D, *c*). In the uppermost fertile whorl the superior corona bears a pair of richly branched hairs (fig. 126 A, D, *h*), but in the others these hairs may be more or less reduced. The gametangia in this species are only joined at the base.

In the case of the classical *Acetabularia mediterranea* (Sect. *Acetabulum*) (fig. 126 F, G; 127 A), whose development is known in all its details,[1] two or three years pass before the plants become fertile. In the first year the zygote produces only an upright usually unbranched cylindrical thread, anchored to the rock by a branched holdfast (fig. 127 J). From this a thin-walled, extensively lobed outgrowth (fig. 127 K, *b*) penetrates into the substratum, and this basal vesicle constitutes the perennating portion of the plant in which food-reserves are stored during the summer. In the autumn the upright cylinder dies away and the persisting basal part becomes cut off by a separating wall. In the following spring a new cylinder sprouts out from the underground part and forms one or more whorls of sterile branches at its apex (fig. 127 C).

In the season in which a fertile whorl arises, this is preceded by the production of a single sterile whorl which is shed before the characteristic "umbrella" is fully mature, leaving a ring of small scars on the stalk a little way below the latter (fig. 127 G, *st*). The umbrella is composed of completely joined elongate gametangia (*g*), the bases of which are enclasped by a pair of likewise fused outgrowths (*coronae*) appearing as small rings when viewed from the surface (fig. 126 F, G). In the young condition each superior corona (fig. 127 G, *s*) bears a polytomously branched lateral (*h*) and often one or two rudiments of further branches, but these are all shed as the gametangial whorl flattens out from its primary cup-like form. The outer walls of stalk and umbrella are throughout encrusted with carbonate of lime (accompanied by oxalate of lime, according to Leitgeb (118)), so that dried plants appear quite white. The contents of the gametangia give rise to a large number of thick-walled multinucleate cysts (fig. 127 B, M) which are set free as the umbrellas disintegrate in the autumn. They remain dormant until the following spring when the gametes are liberated by the detachment of a special lid (fig. 127 N).[2] A fossil species of *Acetabularia* (*Acetabuloides*) is known from the Oligocene.

According to Hämmerling (83, 84) the vegetative plant contains only a single huge, often lobed nucleus (fig. 10 D, p. 70) which is located in one of the branches of the rhizoid. When cyst-formation sets in, this nucleus divides into numerous small ones which are carried by proto-

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[1] See (8), (83), (84), (146) p. 376, (192), (226).

[2] According to Schussnig (181) in *A. Wettsteinii* the cysts set free gametes as soon as they are liberated.

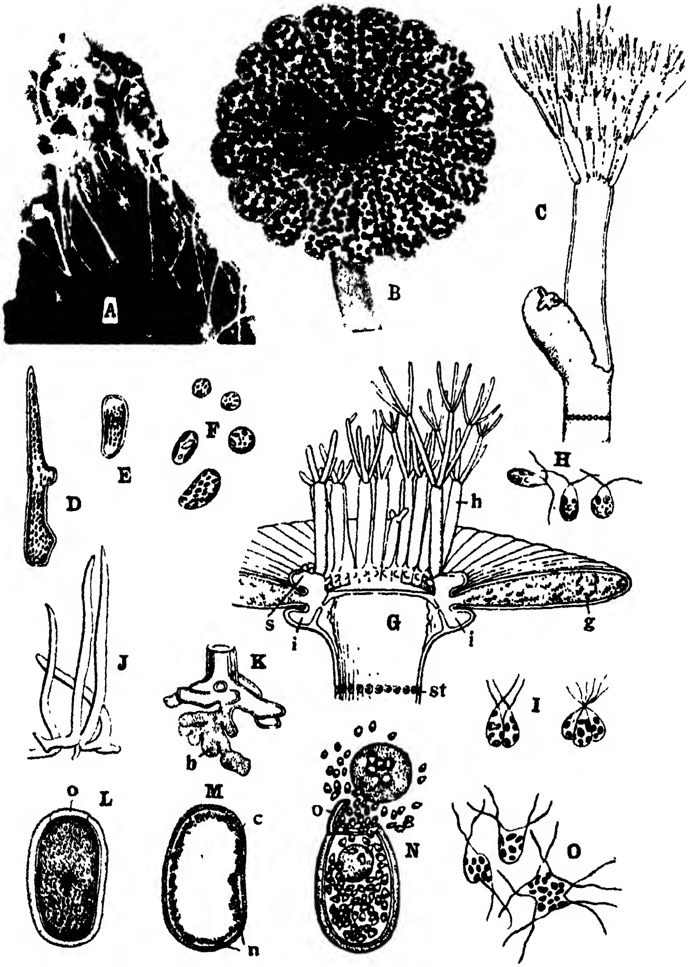

Fig. 127. B, *Acetabularia Wettsteinii* Schussn., umbrella from above, with cysts. A, C–O, *A. mediterranea* Lamx.; A, group of mature plants; C, new shoot arising from remains of stalk; D–F, germinating zygotes; G, structure of young head, partly diagrammatic; H, gametes; I, O, sexual fusion; J, young plants derived from zygotes; K, base of stalk with rhizoids and perennating vesicle (*b*); L–N, cysts; L, intact, with lid (*o*); M, longitudinal section of same; N, liberation of swarmers. *c*, wall of cyst; *g*, gametangium; *h*, sterile shoots; *i*, inferior and *s*, superior coronae; *n*, nucleus; *o*, lid of cyst; *st*, sterile whorl. (A original photo, R. Cullen; B after Schussnig; C after Woronin; G after Oltmanns; the rest after De Bary & Strasburger.)

plasmic streaming into the gametangia; the young cysts are uninucleate. As in other Siphonales, *Acetabularia* shows a great capacity for regenerating lost parts from portions containing the nucleus; removal of the umbrella results in almost all cases in its replacement from the stump of the stalk (84). The chloroplasts are stated (120) to contain a number of granules of carotin distinct from the green pigment and to lack starch. In the ultimate branches the chloroplasts assume a narrow thread-like form.

The closely allied genus *Acicularia* (21, 24, 92, 192) is distinguished by the fact that lime is deposited also in the cavity of each gametangium so that, when the head disintegrates, there remain a number of calcareous spicules, pointed at one and rounded at the other end and honeycombed by numerous cavities containing the cysts (fig. 126 C). This genus was first discovered in the fossil condition as isolated spicules, sometimes laterally connected, which were assigned to diverse positions in the animal kingdom until Munier-Chalmas (129) recognised their probable nature and suggested a close affinity with *Acetabularia*, a view which was subsequently confirmed by the discovery of the single living species.

The Acetabularieae are usually interpreted as Dasycladaceae in which the gametangia are borne laterally on the primary branches (cf. *Bornetella*), but as a result of great enlargement have shifted into the terminal position, the later branches of the lateral being pushed aside on to the adaxial side (192). This falls into line with Svedelius's views as to the primitiveness of the lateral position of the young gametangium in *Neomeris* (p. 393). On this interpretation the superior corona is the part of the primary lateral that bears the further branches, while the inferior corona has to be regarded as a new development.

THE FOSSIL DASYCLADACEAE

While a comparative study of the living members of the family thus serves to link the various forms with one another, the numerous fossil representatives[1] have rendered their relation much clearer and have given us a picture of the progress of evolution which is almost unique. Many of these forms probably played a rôle in the formation of limestone rocks. They are mostly preserved as small cylindrical calcareous tubes pierced by canals (fig. 128 H), from whose arrangement, shape, and mode of branching it has been possible to deduce the habit of the plant. Many of the more ancient types lack the specialised reproductive organs of the modern forms. Only a few selected examples can be considered.

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[1] For the more important literature, see (6), (127), (148–151), (152*a*), (153), (167), (196).

In the oldest known Dasycladaceae (e.g. *Rhabdoporella*(198)) (fig. 128 A) the unbranched laterals of the elongate main axis were quite irregularly disposed and did not fit closely together. Some few (e.g. *Vermiporella*(149, 198)) are distinguished by branching of the main axis. In *Coelosphaeridium* (Ordovician) the branches arose only from

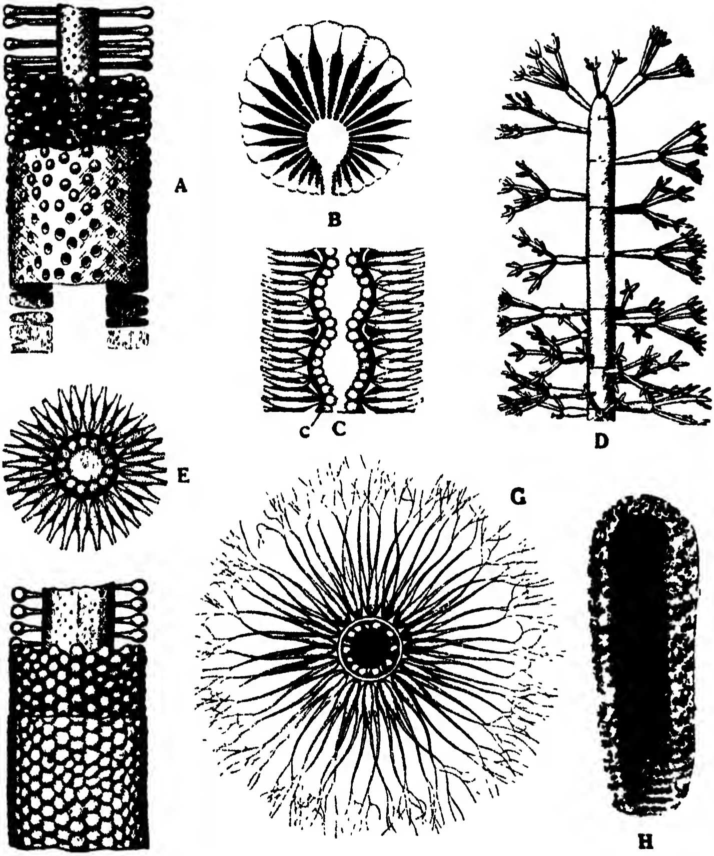

Fig. 128. Fossil Dasycladaceae. A, *Rhabdoporella pachyderma* Rothpl. (Upper Silurian). B, *Coelosphaeridium cyclocrinophilum* Röm. (Ordovician). C, E, G, *Diplopora phanerospora* Pia (Trias?); C, E, longitudinal and transverse sections respectively; G, a whorl, partly restored. D, *Primicorallina trentonensis* Whitf. (Ordovician). F, *Gyroporella vesiculifera* Gümb. (Upper Trias). H, *Dactylopora cylindracea* Lmk. (Eocene). *c*, cysts. (B after Stolley; F after Diener; H after Morellet; the rest after Pia.)

the globular apex of the main axis and their dilated ends were compacted to form a spherical surface (fig. 128 B). *Primicorallina*, from the same formation, has the laterals irregularly and loosely disposed on the elongate main axis, but in this case they are branched to the third degree and are remarkably like those of a *Dasycladus* (fig. 128 D). In the Permian genus *Mizzia* (149) the thallus was composed of a series of segments having the structure of *Coelosphaeridium*. It is presumed that in all these forms the reproductive cells were formed in the main axis (Pia's endosporic type).

In the Mesozoic whorled types appear. The Triassic *Gyroporella* (fig. 128 F) (149) has unbranched laterals with dilated globular apices which are regarded as reproductive. *Diplopora* (149, 152) (fig. 128 C) has the lateral members grouped in tufts, usually of 3–6 members, the tufts being arranged in whorls (fig. 128 E). The laterals were sometimes prolonged into branched hairs (fig. 128 G) and appear often to have functioned as gametangia (Pia's cladosporic type), although in *D. phanerospora* Pia (149), for instance, cysts were formed within the periphery of the main axis (fig. 128 C, E). In *Triploporella* (fig. 129 A) (including *Tetraploporella* (197)), from the Jurassic and Cretaceous, the club-shaped plants bore densely aggregated whorls with elongate broadened primary branches forming numerous cysts (*c*) and bearing three slender secondary branches (*s*) ending in branched hairs (*h*) (cf. also (149), (196), (210)). This genus might well be the starting-point for most of the modern forms, although in Pia's opinion (149) the Dasycladeae go back to the Liassic *Palaeodasycladus* (fig. 129 B), which is perhaps a *Primicorallina* with whorled branching. In *Thyrsoporella* (Eocene) the secondary and even the tertiary branches were enlarged and presumably formed cysts.

Definite reproductive organs (Pia's choristosporic type) appear first in the Cretaceous forms. In *Dactylopora* (Eocene) the unbranched laterals have dilated ends forming a faceted surface, numerous small rounded gametangia being borne on the sides of their narrower inner portions (fig. 128 H). In *Digitella* the gametangia are larger and filled with a mass of lime in which small cavities occur which were no doubt occupied by cysts. The lateral position of the gametangia in these fossil types lends support to the view that the terminal position seen in several of the recent genera is secondary.

The oldest known Dasycladaceae appear to have had their chief centre of distribution in the Arctic, whilst from the Trias onwards they are mainly represented in the Tropics (149). A common plan of construction is recognisable throughout, since all the forms exhibit a but rarely branched main axis upon which the numerous laterals were borne. These were at first irregularly disposed and commonly unbranched, while the cysts were probably formed in the main axis itself. Subsequently, in the Mesozoic, the whorled arrangement was adopted and extensive branching of the laterals became the rule, while the production of cysts was relegated to the enlarged primary branches or sometimes to the secondary ones. In the first place the faceted surface was formed by the primary members, but later, as in the recent genera, by the secondary ones. Ultimately special gametangia were differentiated, first as lateral appendages to the primary branches and subsequently as single terminal structures at the ends of the latter. The recent genera (*Neomeris*, *Cymopolia*, *Acicularia*) first appear in the Cretaceous (150, 196). In view of this evolutionary sequence, for a knowledge of which we are mainly indebted to Pia, the early stages of *Neomeris* and *Acetabularia* appear to represent a reversion to a more primitive condition, and it is

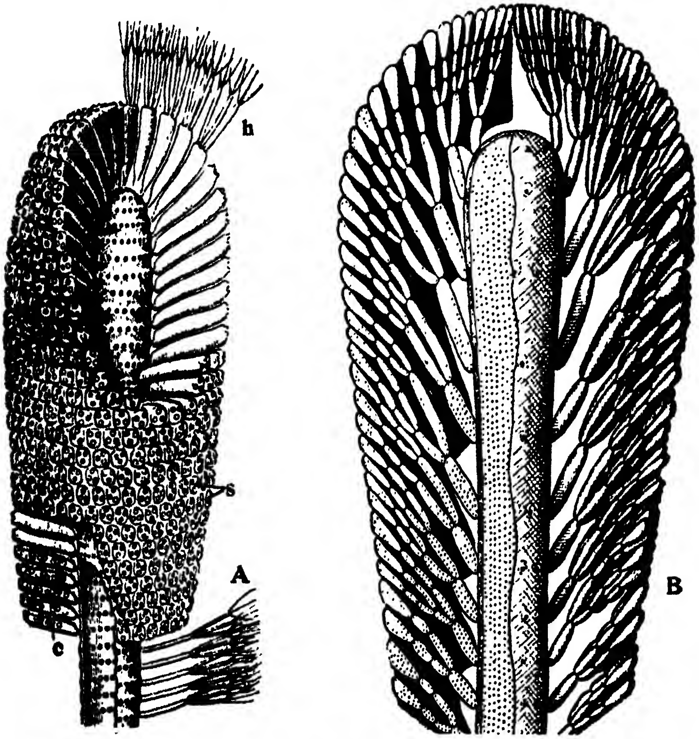

Fig. 129. A, *Triploporella* (*Tetraploporella*) *Remesi* Steinm. (Upper Jurassic), reconstruction (after Steinmann). B, *Palaeodasycladus mediterraneus* Pia (Lias) (after Pia). *c*, cysts; *h*, secondary branches; *s*, scars of secondary branches.

significant that in young plants of the former it is at first the ends of the primary branches that become dilated to form an imperfect cortex. According to Pia (150) parallel evolution has played a great rôle in this family; in particular, the specially differentiated gametangia appear to have arisen independently in a number of lines, and their geological history shows that they are organs *sui generis* and not modified members of the whorls.[1]

THE REPRODUCTION OF THE DASYCLADACEAE

Throughout the preceding matter the reproductive organs have been described as gametangia, although the fate of their contents is known only in a very small number of cases. Since, however, in all of these they have proved to subserve sexual functions, the uniform designation is warranted until there is proof to the contrary. Printz (158) speaks, however, of aplanosporangia and of the cysts as aplanospores.

In *Dasycladus*, in which the gametangia are not included in the calcareous envelope, the gametes are produced directly, but in all the more advanced, and in general more strongly calcified, forms the contents give rise to one (*Neomeris*) or usually several (e.g. *Acetabularia*) resting cysts from which gametes are mostly only set free after shedding. In fact the production of cysts, which clearly obtained already in the fossil forms, appears as a necessary adaptation to the development of a more or less complete calcareous envelope. Pia ((149) p. 163) regards the condition found in *Dasycladus* as secondary.

The sexual reproduction is in all cases isogamous by means of biflagellate gametes. Those of *Dasycladus* (fig. 123 B, p. 388) are prominently flattened and are somewhat rectangular when viewed from the broad surface; those of *Acetabularia* (fig. 127 H) are ovoid. The zygotes usually germinate immediately and grow directly into a new plant (fig. 127 D–F). When there is a resting stage in the life-cycle of the Dasycladaceae it is constituted by the cysts and not by the zygote. In *Cymopolia* the gametangia fall off as a whole and appear to germinate directly (191), a state of affairs that has been interpreted as apogamy (35). There is little doubt that the Dasycladaceae, like the Codiaceae, are diploid organisms and Schussnig (178) states that he has established reduction in the cysts of *Acetabularia* during gametogenesis.

Dasycladus is dioecious (9), although Jollos (105) found occasional monoecious plants. The latter established that there was much variation

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[1] Florin's *Piaea* (68), from the Permian, may, in view of its whorled branching, be a member of the Dasycladaceae, but the fact that the various axes apparently consist of rows of cells and that the long laterals are axillary to the whorls indicates a possible relation to Charales (cf. (153*a*) and p. 465).

in the intensity of the sexual reaction when gametes from different individuals were brought together, copulation sometimes occurring immediately, sometimes only after a more or less prolonged interval; in the latter case the zygotes passed through a resting period before germination. Gametes exhibiting such weak sexual tendencies were capable of fusing with either strain of gamete possessed of stronger tendencies (relative sexuality, cf. p. 44 and *Ectocarpus siliculosus*). When gametes of a weak strain were placed in water that had been filtered off from gametes of a strong opposite strain, the sexuality of the former was altered in the direction of that of the latter. In *Acetabularia* also it is only gametes from different cysts (from different individuals?) that normally fuse with one another.

(*e*) THE FAMILY CODIACEAE

Vegetative Structure

The members of this family are composed in the mature condition of a system of richly branched threads which, in the more specialised types, are more or less completely agglomerated to form a compact parenchymatous body (multiaxial construction). All these threads are products of a single primary filament. The main threads exhibit apical growth and are dichotomously branched (figs. 130 D, 131 B), but in most genera there is also an abundant formation of laterals (figs. 130 E, 131 F) which play a considerable rôle in binding together the main threads and whose formation in smaller or larger numbers sets in as soon as aggregation of the latter commences. In most genera the main threads exhibit more or less frequent constrictions, especially near the points of branching (figs. 130 D, 131 B), and at these points there are stratified annular thickenings (fig. 131 E) of the wall which sometimes almost meet in the centre (124). The probable mechanical function of these thickenings is indicated by their absence in the more firmly built parts. The structure of the threads is typically siphoneous, but the small chloroplasts in most genera lack pyrenoids; the nuclei lie as usual internal to the chloroplasts. The membranes consist in the main of callose and pectin (124), although according to Ernst ((50) p. 121) the thickenings contain cellulose; in *Codium* pectin is stated to preponderate.

Like the Dasycladaceae the Codiaceae have their chief centre of distribution in the warmer seas, although a number of genera are found in the Mediterranean and *Codium* extends as far north as Alaska and Norway and southwards to Cape Horn and Kerguelen.

One of the simplest members is *Rhipidodesmis* (75), with a solitary species found in the Indian Ocean. Here we have a heterotrichous habit, the creeping system of irregularly branched and almost colour-

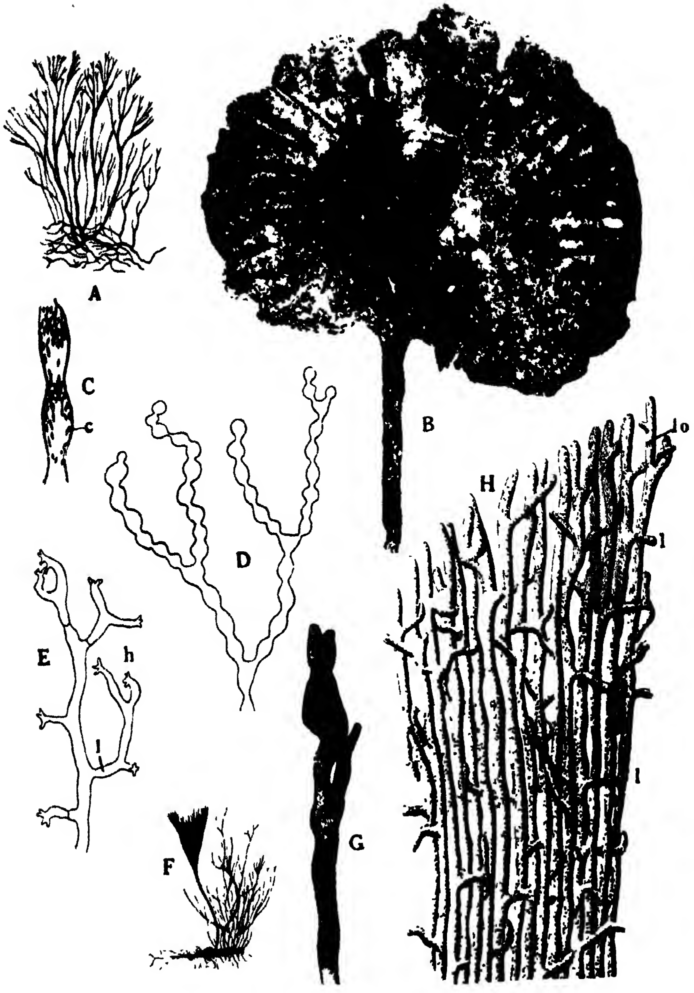

Fig. 130. Codiaceae. A, *Rhipidodesmis caespitosa* (J. C. Ag.) Gepp, habit. B, *Avrainvillea asarifolia* Boerg., habit. C, D, *A. nigrescens* Decsne., portions of the threads. E, *Rhipilia tomentosa* Kutz., threads from surface of thallus with haptera (*h*). F–H, *Udotea minima* Ernst; F, habit; G, early stage of stalk-formation; H, edge of fan at a period of intensive growth, the longitudinal threads (*lo*) becoming bound together by laterals (*l*). *c*, chloroplast; *l*, lateral branches. (A after Gepp; F–H after Ernst; the rest after Boergesen.)

less threads giving rise to a considerable number of erect filaments with abundant di- or trichotomous branching in their upper portions and all growing approximately to the same height (fig. 130 A). This simple form can be instructively compared with *Caulerpa fastigiata* (p. 378). *Boodleopsis* (75) is similar, but the upright filaments are far more richly branched and aggregated to form a cushion.

In other forms the habit is more definite. Thus, in the tropical genus *Avrainvillea* (20, 24, 75, 136) the dichotomously branched filaments are generally united below to form a loose cylindrical stalk, anchored by colourless rhizoids and sometimes forked one or more times; at the top the threads spread out and interweave to form a leaf-like flabellate expanse with an entire or lobed margin (fig. 130 B). The numerous constrictions in the threads forming this blade give them a moniliform appearance (fig. 130 C, D). *Rhipilia* (Atlantic and Indian Oceans) (24, 75) shows much the same habit, but exhibits greater specialisation in that the threads (fig. 130 E) composing the blade bear short laterals developing small lobes (*h*) at their apices by means of which they attach themselves to the neighbouring threads.

This is more elaborated in *Udotea* (including *Flabellaria*), as is clearly shown by the two Mediterranean species. In *U. minima* Ernst (60) the coarse colourless creeping threads produce numerous erect dichotomous filaments which are in part quite free, but at certain points become interwoven (fig. 130 G) to form a short stalk at the top of which they either diverge to form a brush-like tuft or commonly spread out to form a small flat fan (fig. 130 F); the threads of both stalk and fan bear short and irregularly branched laterals which arise more or less perpendicularly along either surface of the fan and spread out to form an imperfect layer, serving to bind the whole together (fig. 130 H). Young stages of this form may be compared with *Rhipidodesmis*, older ones with *Penicillus* (cf. p. 406) and *Avrainvillea*.

In *Udotea Desfontainii* (Lamx.) Decsne. (*Flabellaria petiolata* Trev.), which grows in very diverse habitats in the Mediterranean (60, 116), the early stages (fig. 131 C) are very much like those of the species just described, although the threads composing the rhizome as a general rule soon become interwoven into bundles. The mature fans (fig. 131 A) are larger and possess a firmer structure, since the ramuli in this case are richly lobed (fig. 131 H) and become apposed to either surface of the fan to form a more perfect covering which in parts recalls the strongly undulate epidermis of the leaf of a higher plant. The fans are thus three-layered, with a central axis of longitudinal threads and a cortical layer of laterals on either side (cf. fig. 131 F). Some of the laterals also push in between the axial threads, bending them considerably out of their course. The darker concentric zones visible on the fans (fig. 131 A) indicate points at which there is an especially strong development of extensively lobed ramuli which here form a complete covering and in part even project from the surface, whereas in the intervening lighter zones the covering is not so perfect, so that the axial threads are partly exposed. In the stalk too the

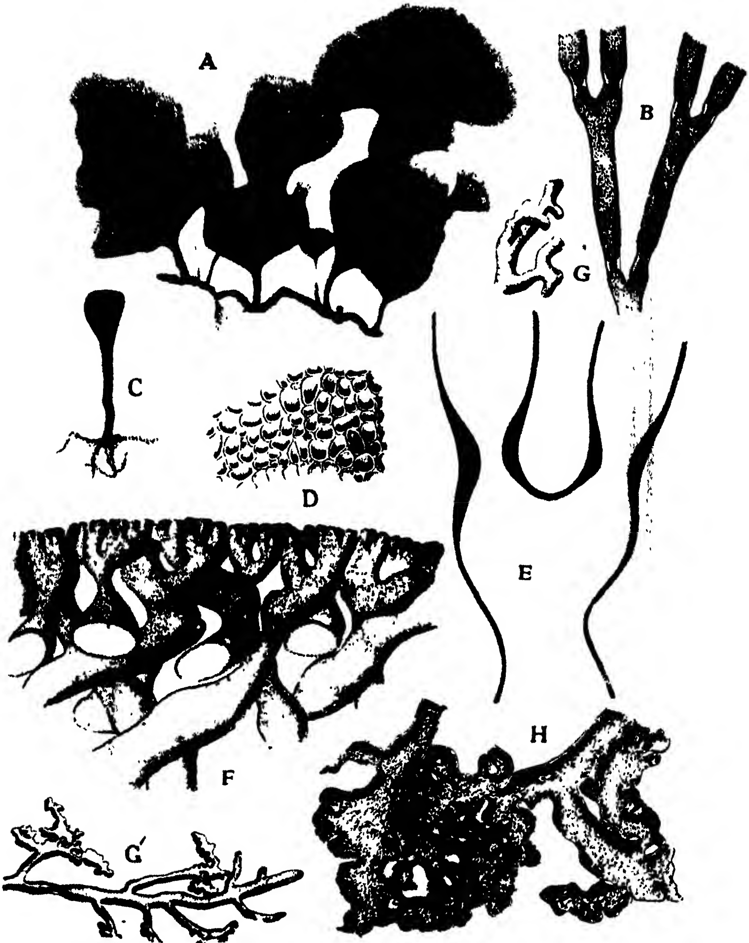

Fig. 131. *Udotea Desfontainii* (Lamx.) Decsne. (after Ernst). A, mature plant; B, part of a longitudinal thread; C, young plant, stalk broadening out to form fan; D, cortication of surface of stalk; E, point of forking of longitudinal thread, showing thickenings; F, surface of stalk in transverse section showing cortex-formation; G, G′, apices of medullary threads with laterals; H, lobing of laterals of two longitudinal threads.

laterals in this species form a more or less complete envelope, but here both they and their numerous branches stand perpendicular to the axial threads (fig. 131 F), the ultimate lobes fitting closely to form a cortex which in surface view appears composed of rounded elements (fig. 131 D).

In both species the axial threads composing the fans lose the characteristic constrictions and internal thickenings, are narrower than the free threads, and also differ in the abundant production of laterals. At the edge of older fans, prior to the cessation of growth, the axial threads usually project as a free fringe (fig. 131 A), and such projecting threads revert to the characters of the young non-agglomerated ones. In *U. Desfontainii* secondary fans often arise from the margin or surface of the primary ones.

The tropical species of *Udotea* (24, 75, 96, 231) are more or less encrusted with lime, and most of them exhibit a more elaborate development of the cortical layers. In *U. javensis* (75) the long stalk is composed of but a single thread which subsequently becomes overgrown with rhizoids.

The fan-structure is most highly perfected in *Halimeda*,[1] in which the branched thallus is composed of a number of usually flat (often cordate or reniform), strongly calcified segments; these are separated by uncalcified joints and arise from a short basal stalk attached to the creeping system (fig. 132 D). *H. Tuna*, which is but slightly calcified, occurs commonly in the Mediterranean. Species of *Halimeda* may play a considerable rôle in the formation of some coral-reefs (34) and are known from the Tertiary onwards. The lateral branches of the axial threads in this genus stand perpendicularly, as in the stalk of *Udotea*, and their ultimate branchlets swell up and become closely adpressed to one another to form a very compact surface with hexagonal facets (fig. 132 G, *f*). The lime is deposited on the side walls of these facets, the outer surfaces against which the chloroplasts lie being free from incrustation. When new segments of the thallus are to be produced, the axial threads grow out at the apex of the segment in one or more groups and, since ramuli are not formed immediately, a bare uncalcified joint lacking laterals is formed between the segments; the threads forming the joints have strongly thickened walls (cf. *Corallina* among the Red Algae).

Of the diverse specialised types that belong here one of the most remarkable is the West Indian *Rhipocephalus* (74, 75), in which the upper part of the calcified stalk bears numerous closely crowded flabellae (fig. 132 B, C), each formed by periodic lateral protrusion of groups of the longitudinal threads composing the stalk.

A different habit is seen in *Penicillus* (*Espera*) (24, 74, 75, 226), of which *P. mediterraneus* Thur. forms extensive meadows on muddy substrata

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[1] See (5), (7), (22), (24), (94), (95).

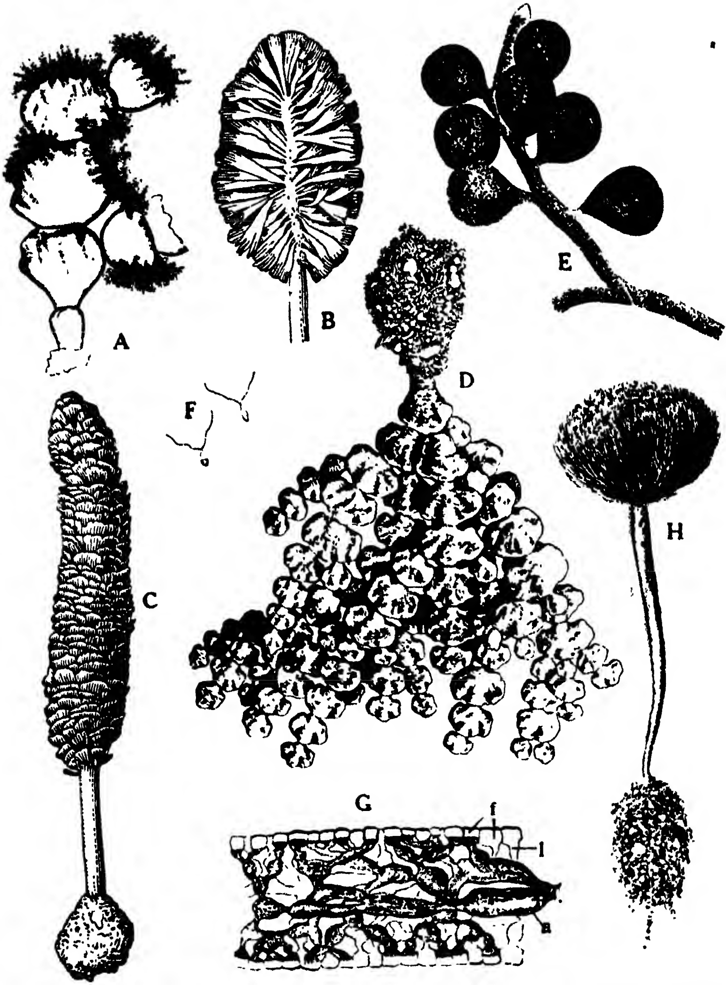

Fig. 132. A, E, F, *Halimeda Tuna* (Ellis et Sol.) Lamx.; A, about natural size, with gametangial branches; E, one of the latter enlarged; F, swarmers (gametes?). B, C, *Rhipocephalus phoenix* (Ellis et Sol.) Kütz.; B, section; C, entire plant, about natural size. D, *Halimeda incrassata* (Ellis et Sol.) Lamx. var. *simulans* (Howe) Boerg., about natural size. G, *H. Opuntia* (L.) Lamx., longitudinal section of a segment. H, *Penicillus capitatus* Lamx., about natural size. *a*, longitudinal threads; *f*, facets; *l*, laterals. (A, E, F after Derbès & Solier; B, C after Gepp; G after Goebel; the rest after Boergesen.)

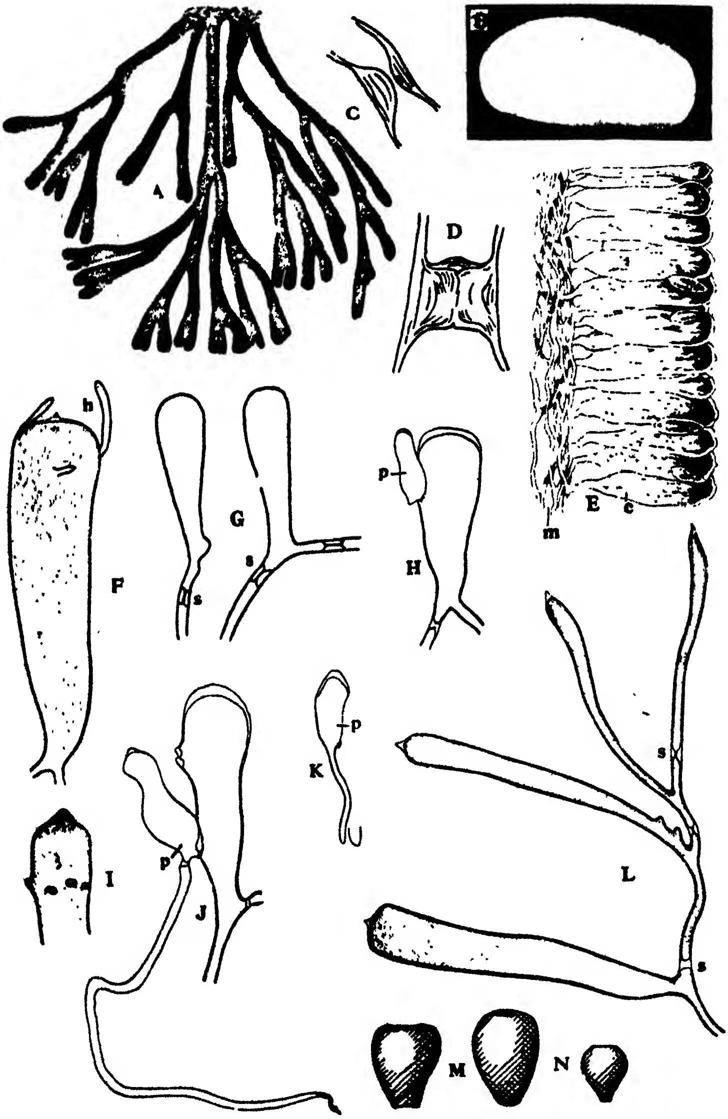

Fig. 133. A–L, *Codium*. A, C, E, G, *C. tomentosum* (Huds.) Stackh.; A, habit; C, septum-formation; E, part of a longitudinal section; G, septum-formation

within which the felt of branched rhizomes ramifies. These at first produce separate upright threads of the usual type which later unite to form a calcified stalk showing a well-marked differentiation into central medulla and cortex; the main threads develop numerous laterals which in part wind transversely between them and bind the whole together. At the apex of the stalk the central threads separate to form a brush-like tuft of forked filaments which, as in the other cases above considered, revert to the normal type of structure found in the young plant (fig. 132 H).

The general structure is somewhat different in the uncalcified genus *Codium*,[1] of which the widely distributed *C. tomentosum* and *C. Bursa* are amongst others found in northern waters, although many species are confined to warmer seas. They typify the principal habits met with in the genus. In *C. tomentosum* (fig. 133 A) the thallus, firmly anchored by a basal disc, consists of cylindrical hairy segments which are about the thickness of an ordinary lead-pencil and repeatedly forked; they float out into the water or hang down from the rocks at low tide. In *C. adhaerens* (Cabr.) Ag. the thallus is a flat cushion or crust attached by numerous rhizoids along the under side, while in *C. Bursa* it appears as a large rounded structure (10–20 cm. in diameter), slightly flattened at the point of attachment to the substratum (fig. 133 B) and becoming hollow at maturity; within the hollow may be found diverse small animals and red-coloured Myxophyceae (69, 208).

In *C. tomentosum* the thallus in section (fig. 133 E) is seen to be composed of a central medulla (*m*) of longitudinal, rather narrow, interwoven, forked threads and a peripheral cortex (*c*) of large club-shaped vesicles densely grouped at the same level to form a palisade-like layer. Chloroplasts are aggregated in large numbers beneath the outer surface of each cortical vesicle (fig. 133 E) and are also found in the hairs which are produced periodically on these structures (fig. 133 F), and give the plant its tomentose character (cf. (184)); when they drop off they leave characteristic scars (fig. 133 I).

In longitudinal sections it is usually not difficult to recognise that the vesicles represent the dilated terminations of one of the forks of

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[1] See (76), (98), (116), (146) p. 396, (170), (205), (216).

in relation to vesicles. B, D, *C. Bursa* (L.) Ag.; B, habit, somewhat reduced; D, septum-formation. F, I, L, *C. mucronatum* J. C. Ag.; F, vesicle with hairs; I, the same with scars of hairs; L, longitudinal thread and vesicles, showing sympodial construction. H, J, K, *C. isthmocladum* Vickers; H, J, formation of propagules (*p*); K, one of the latter. M, N, *Ovulites*; M, *O. margaritula* Lmk.; N, *O. pyriformis* Schwag. *c*, cortical vesicles; *h*, hairs; *m*, medullary threads; *s*, thickenings of wall. (A, E after Gibson & Auld; B original photo, R. Cullen; C, D, G after Küster; F, I, L after Hurd; M, N after Pia; the rest after Schmidt.)

a longitudinal medullary thread (fig. 133 G, L). From the base of the vesicle one or several branches arise, some of which grow more or less transversely and help to bind the medullary threads together, whilst others grow lengthwise between cortex and medulla and sooner or later curve out afresh and become dilated to form another cortical vesicle (fig. 133 L). At the base of each of the latter, as well as at the points where these lateral branches are given off, one finds the customary annular thickenings (fig. 133 G, L, *s*); these are so strongly developed that they seem to meet (fig. 133 D), although according to Mirande (124) a delicate plasma strand traverses them through which transport of material can take place (117*a*); in *C. Bursa* the pores are stated to become widened in spring, but to become narrowed again in autumn.

The zygote of *Codium* (p. 411) germinates to form an upright thread attached at its base by a lobed sucker (fig. 134 N). At an early stage thin branches arise from the lower end of the primary thread and these soon swell at their tips and bend out to form the first vesicles (fig. 134 M), whilst their longitudinal growth is continued by branches originating from the bases of the vesicles ((146) p. 398, (170)). The *Codium*-plant is therefore built up of the ramifications of a single initial filament and the entire construction is sympodial, the vesicles being the laterally deflected apices of the longitudinal threads whose further growth is effected by side branches.

The growth in length of the diverse segments of the thallus in *C. tomentosum* is effected by apical elongation of the medullary threads, but the continuous intercalation of fresh cortical vesicles between the pre-existing ones not only leads to their dense apposition, but also brings about a certain amount of intercalary enlargement. In the cushion-like forms, in which the laterals from the bases of the vesicles grow in a more or less tangential direction, this growth by intercalation predominates and, as the thallus increases in girth, the surface becomes more and more stretched. This leads to the rupture of the internal threads, so that older plants of this type are often hollow.

The South African *Pseudocodium* (213) has the same habit as *C. tomentosum*, but here the vesicles are apparently true laterals of the medullary threads. This genus also resembles *Halimeda* in the fact that the vesicles are so densely crowded that they form a system of polygonal facets.

The few fossil members of the Codiaceae do not afford much help in elucidating the phylogeny of the family. Several genera are known from the Lower Silurian, e.g. *Palaeoporella* (151, 198), in which the thallus consisted of segments separated by uncalcified joints, the former composed of richly branched threads whose ends formed a thin cortical layer. *Dimorphosiphon* (91), with terete joints, is very similar to some kinds of *Halimeda*, while *Boueïna* (Cretaceous) (162, 195) appears as a closely allied form. *Ovulites* (Eocene) (129, 187 a) is believed to represent the calcareous body of an alga allied to *Penicillus*; it occurs as small ovoid or rod-shaped hollow bodies (fig. 133 M, N) whose wall is perforated by numerous fine pores and which have a large aperture at either end (cf. also (33)). Glück's *Microcodium* (77) from the Miocene is not yet certainly established. Some genera that have been referred here (e.g. *Sphaerocodium* (167) p. 296) are very doubtful (cf. (187 a) p. 160).

Pia (153 a) believes in a close relationship between Dasycladaceae and Codiaceae, basing this view on the fact that some of the oldest Dasycladaceae have an elongate axis bearing numerous short branches. In some of the Udoteae, moreover, whorled branching occurs.

THE REPRODUCTION OF THE CODIACEAE

Little information is as yet available about the reproduction of the majority of the Codiaceae. Vegetative propagation is no doubt widespread, and in certain species of *Codium* special detachable propagules (fig. 133 H, J, K, *p*) formed on the vesicles have been found (170). This genus is the only one in which sexual reproduction has been reported (146, 203). The gametes are formed in special ovoid gametangia (fig. 134 A–C) which arise as lateral outgrowths from the vesicles, from which they are cut off by a septum like that of *Bryopsis* (p. 377). Two kinds of gametes are formed, either on the same or on different individuals (171), and they are set free by gelatinisation of the apex of the gametangium. Only part of the protoplasm is used in the production of the swarmers. The macrogametes, formed in deep green gametangia (fig. 134 A, B), are pear-shaped and contain numerous chloroplasts with pyrenoids (fig. 134 F), while the microgametes, formed in yellowish gametangia, are narrower and possess 1–3 small yellowish chloroplasts without pyrenoids (fig. 134 E). Both have two flagella. Fusion is followed by the formation of a rounded zygote (fig. 134 G) which germinates at once (fig. 134 L) in the way described on the previous page. The macrogametes are stated to be able to germinate without fusion.

Williams (222) has shown that reduction in *C. tomentosum* takes place during the first nuclear division leading to the formation of gametes (fig. 134 H, J), so that the thallus in this species is diploid, as in other Siphonales that have been investigated from this point of view; this has since been confirmed for *C. elongatum* (178, 182). According to Williams some of the nuclei that pass into the gametangia disintegrate, the selection of the functional nuclei being apparently related to their proximity to certain deeply staining cytoplasmic centres, smaller than the nuclei, which are compared to the coenocentra recorded in Oomycetes. The surviving nuclei undergo two simultaneous nuclear divisions, the first of which effects reduction.

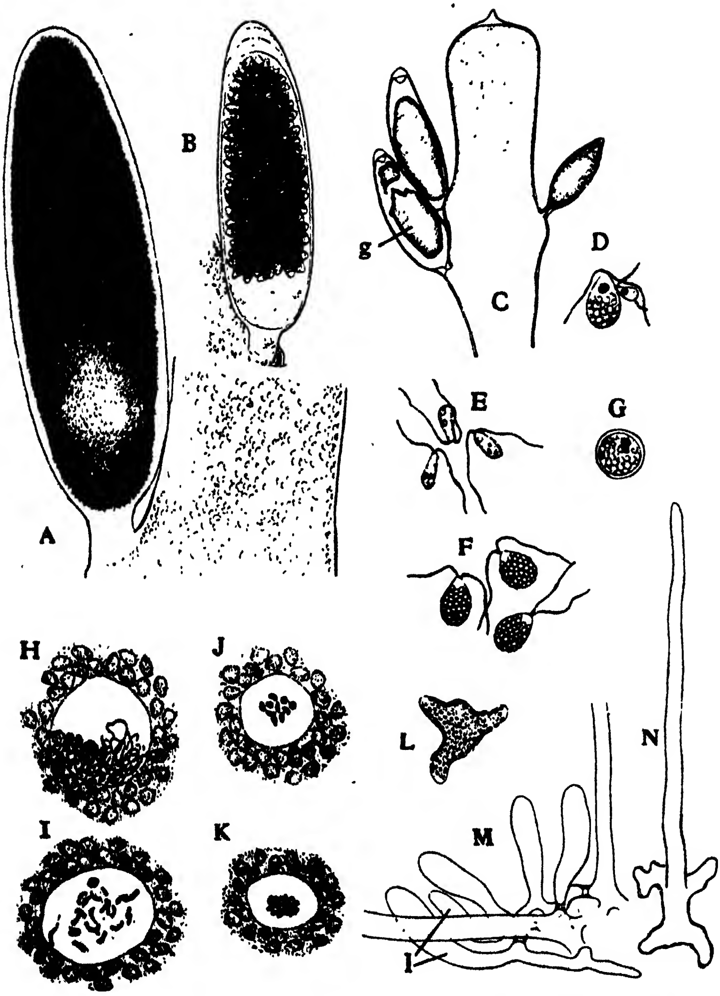

Fig. 134. Reproduction of *Codium*. A, B, D–N, *C. tomentosum*; C, *C. mucronatum*. A, young and B, mature gametangium; C, vesicle with three gametangia; D, sexual fusion; E, micro- and F, macrogametes; G, zygote; H–J, meiosis in gametangium, H, late synapsis, I, diakinesis, J, metaphase (polar view); K, late prophase in vegetative nuclear division (polar view); L, early stage in germination of zygote; M, basal part of young plant; N, germling. *g*, gametangium; *l*, vesicle. (A, B after Thuret; C after Hurd; H–K after Williams; the rest after Berthold from Oltmanns.)

Special reproductive organs have also been observed in *Halimeda* 73,95,174), although their function is not clear. They are formed on forked threads that sprout out in large numbers from the edges of the calcified segments or from their surfaces (fig. 132 A, p. 407) and represent a proliferation of the axial filaments. These reproductive threads bear numerous spherical outgrowths which receive almost the entire contents of the segment on which they are borne (fig. 132 E), but in some species at least are not cut off by septa. Small biflagellate swarmers (fig. 132 F) are produced in large numbers in the outgrowths, as well as in the adjacent threads, the process even extending back into the axial filaments of the segment below. The fate of these swarmers is not known, but, since they have been observed to perish rapidly without becoming enveloped by a membrane, they are possibly gametes.

In *Avrainvillea* (95) club-shaped sporangia (?), formed terminally on the blade and giving rise to 1–8 spores, have been observed. So-called reproductive organs reported for *Udotea* and *Penicillus* have proved to be epiphytic organisms ((60) p. 231).

(*f*) THE FAMILY VALONIACEAE

VEGETATIVE STRUCTURE

The common characteristic of the members of this family lies in the fact that the primary coenocytic vesicle at an earlier or later stage becomes divided into more or less numerous multinucleate portions which give it a multicellular character. Whether all the diverse forms included here really constitute a natural group is not yet quite clear. The peculiar method of segregative division (cf. p. 415), by means of which the multicellular condition is attained, and the usual grouping of the lobed chloroplasts, only some of which contain pyrenoids, to form a network (figs. 135 C, 136 L) speaks, however, for a certain affinity. Some of the less specialised types are very closely related to the Protosiphonaceae, so that they might with almost equal justification be included in that family.

This is very true of many species of *Valonia*,[1] the majority of which inhabit tropical and subtropical seas, although a few are found in the Mediterranean. The young plants in all cases consist of a macroscopic, often club-shaped vesicle anchored basally by rhizoids of various types (fig. 135 A) and possessing the usual siphoneous structure; the lobed chloroplasts are characteristically arranged in a network (fig. 135 C). At later stages the protoplasm and chloroplasts

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[1] See (23), (24), (64), (112), (113), (134), (172), (173).

mass at certain points, and these accumulations, which usually appear circular when viewed from the surface, secrete a membrane the outer part of which is contiguous to and becomes confluent with that of the main vesicle ((18) p. 264, (64) p. 342). In this way more or less numerous small marginal cells are formed, which appear to be cut off by arched septa[1] (fig. 135 B, D, *m*). These cells rarely form a connected layer over any considerable part of the surface of the vesicle and are sometimes confined to the basal region, where they are always formed in some numbers and where they grow out into secondary rhizoids with expanded and often lobed apices (fig. 135 B, H, I, *r*).

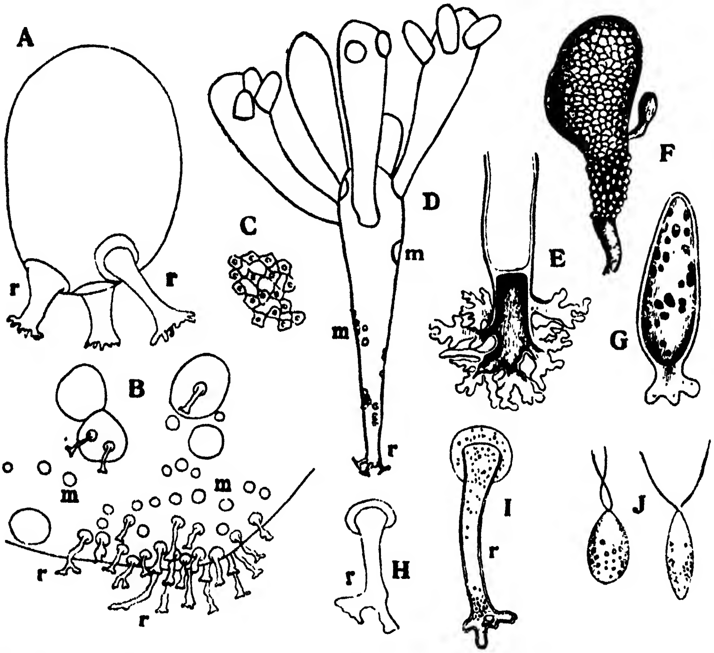

Fig. 135. *Valonia.* A–C, H, I, *V. ventricosa* J. Ag.; D–G, J, *V. utricularis* (Roth) Ag. A, young plant; B, base of an older plant showing marginal cells (*m*) bearing rhizoids; C, group of chloroplasts; D, entire plant; E, apex of one of the older rhizoids of latter; F, swarmer-formation; G, germinating swarmer; H, I, marginal cells with rhizoids; J, swarmers. *m*, marginal cell; *r*, rhizoid. (D after Schmitz; E–G, J after Famintzin; the rest after Boergesen.)

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[1] This recalls in some ways Klebs' observations ((108) p. 190) on *Protosiphon*, where there is an occasional formation of an apical cortex, due to the cutting off by septa of numerous small apical protrusions.

In the West Indian *V. ventricosa*, where the vesicle may attain the size of a small hen's egg, no further development takes place ((24) p. 28), but as a general rule some of the peripheral cells cut off at the apex of the vesicle are of larger size and grow out into branches repeating its structure. Thus, in the Mediterranean *V. utricularis* such branches are frequent and may even give rise to tertiary ones (fig. 135 D). In the tidal zone, however, according to Kuckuck (113), this species may exhibit another growth-form in which the marginal cells are formed especially in the lower part of the primary vesicle and grow out into short creeping branches which turn up at their ends to form secondary vesicles, so that a dense tufted growth is produced. Another species, *V. Aegagropila* C. Ag. (113, 169), known from the Mediterranean and elsewhere, forms loose spherical balls, apparently composed of a number of extensively branched individuals. In short, starting from a common primary type, the diverse species of the genus may ultimately exhibit a very varied habit. The vesicles of *Valonia* show a marked capacity to heal wounds by the growing together of the exposed edges of the protoplast (106, 110).

The tropical genus *Dictyosphaeria*[1] shows a slightly different method of attaining the multicellular condition. The primary, variously shaped vesicles are attached by short rhizoids formed from marginal cells as in *Valonia* (fig. 136 E, F). Later the contents of the vesicle contract and undergo simultaneous division into a number of multinucleate rounded masses (fig. 136 B–D) which secrete membranes independent of that of the parent-vesicle and then enlarge, so that they become pressed against one another (fig. 136 B, H). Each of the "cells" thus formed may later divide again in the same manner (fig. 136 B). The compact mass of somewhat unequal polygonal segments produced in this way is further linked by numerous small interlocking haptera with minute apical processes, arising from small cells cut off from the contiguous faces of the segments (fig. 136 G, H, *h*). Some of the lower segments are produced into tubular outgrowths which are attached by similar haptera to the substratum (fig. 136 H). The mature thalli are large, sometimes slightly lobed vesicles whose surface displays the polygonal outlines of the component segments (fig. 136 A). In some species the inner segments subsequently die, so that the thallus becomes hollow and in such cases it often tears open in older individuals. Localised thickenings of the membrane are frequent.

The method of attaining the multicellular condition, seen in *Dictyosphaeria* and found in many other genera of Valoniaceae, has been styled ***segregative division*** by Boergesen (24). In *Valonia* it is seen in a somewhat modified form, for here the protoplasm masses parietally and the resulting cells become fused with the wall of the

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[1] See (3), (23), (24) p. 33, (42), (133), (215).

parent vesicle. In *Dictyosphaeria* and others, however, the protoplasm aggregates centrally and the segments at first lie freely in the vesicle.

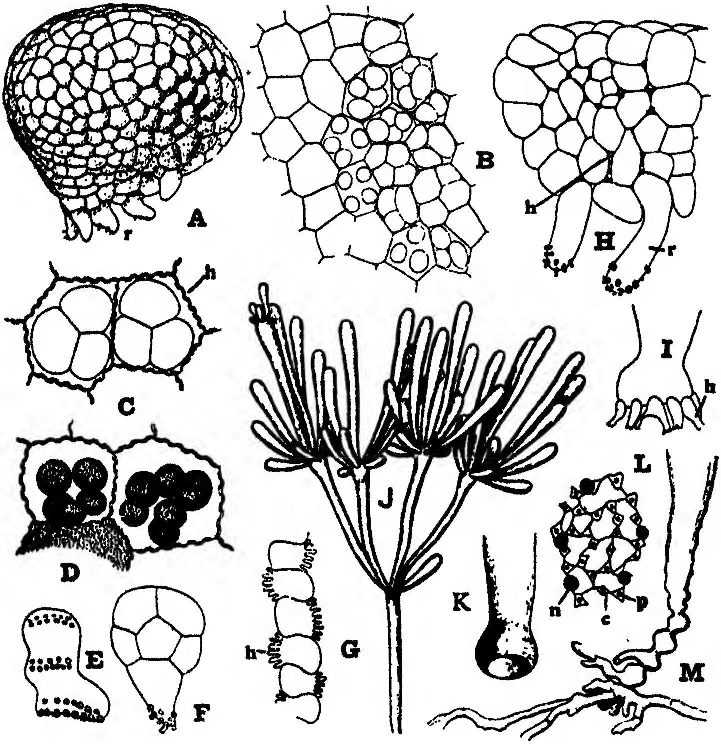

Fig. 136. A–G, *Dictyosphaeria favulosa* (Ag.) Decsne.; A, habit; B, part of thallus, different stages of segregative division; C, D, the same enlarged, D an earlier stage than C;[1] E, F, young plants; G, haptera between two cells seen from above. H, *D. van Bosseae* Boerg., section of young plant showing haptera (*h*) between the cells. I–M, *Ernodesmis verticillata* (Kütz.) Boerg.; I, basal end of branch, with haptera (*h*); J, habit; K, base of a branch; L, chloroplasts and nuclei (black); M, base of plant. *c*, chloroplast; *h*, hapteron; *n*, nucleus; *p*, pyrenoid; *r*, rhizoid (all after Boergesen).

It may not be inappropriate to point out that this mode of septation is markedly different from that of Cladophoraceae, the more as many Valoniaceae show a striking similarity in habit to members of that family. Schussnig (179) regards segregative division as primitive for

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[1] The final stage is seen in B, where some of the segments are dividing afresh.

the Siphonales and believes that in the more specialised types it has become restricted to the reproductive organs.

Boergesen's *Ernodesmis verticillata* (*Valonia verticillata* Kütz.) ((23), (24) p. 67, (113)) again starts as a single narrow clavate vesicle, which exhibits a number of annular constrictions just above the irregularly branched, septate,[1] attaching rhizoid (fig. 136 M). Marginal cells, formed as in *Valonia*, are cut off only at the apex of the vesicle and grow out into narrow clavate branches repeating the structure of the primary vesicle (fig. 136 J) and showing a single annular constriction at the base (fig. 136 K). The branches are formed successively and appear as a whorl in which younger members are always found developing among the older ones (fig. 136 J). Short thick haptera often arise from small cells formed beneath the point of constriction (fig. 136 I); these grow towards the wall of the underlying parent-segment to which they become firmly attached, thus strengthening the whole. They may also serve to attach loose segments to a new substratum. The whorled branching of *Ernodesmis* recalls the Dasycladaceae.

In *Siphonocladus* (18, 24, 94, 172), with *S. tropicus* (fig. 137 B) frequent in tropical seas and *S. pusillus* (fig. 137 A) in the Mediterranean, the small erect plants are attached by a well-branched thick-walled rhizoid (*r*) with or without septa; above this, at the base of the primary vesicle, a number of constrictions are again to be seen (fig. 137 E, F). Sooner or later the vesicle becomes divided into a large number of irregularly arranged cells of unequal size formed by segregative division (fig. 137 H, I), the membranes of these segments subsequently fusing not only with one another but also with the wall of the primary vesicle. From many of these segments outgrowths arise which burst through the thick lamellate membrane of the vesicle at their point of origin (fig. 137 A–C). The branches (fig. 137 C) also show a number of basal constrictions and, although some may remain undivided, others become multicellular in the customary manner (fig. 137 D). Tertiary branches (fig. 137 B) may arise from these in the same way as the secondary ones.

Two specialised tropical forms, *Struvea* and *Chamaedoris*, are readily derived from the type represented by *Siphonocladus*. In the former (23, 24, 28, 135) branched, septate, creeping rhizoids bear a number of long-stalked blades built up of a complex network of branches (fig. 138 A). The stalk represents the primary vesicle and shows the usual basal constrictions. Sooner or later the upper part of the vesicle becomes divided in the customary manner into a linear series of equal segments, of which the uppermost acts as an apical cell by means of which further growth in length, accompanied by segregative division, is carried on. Except for this apical cell each segment of the main

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[1] According to Boergesen ((25) p. 74) this septation also results from segregative division.

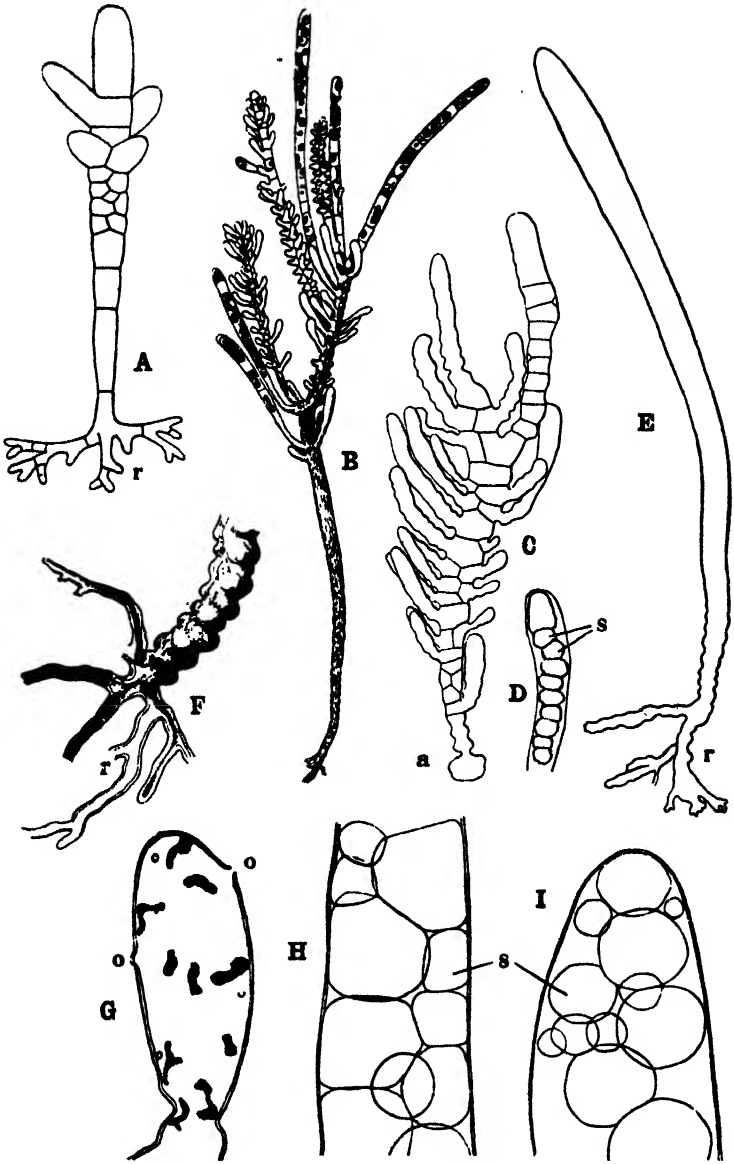

Fig. 137 [*for description see opposite*]

axis puts out, at its upper end, a pair of branches which become divided into a row of segments branching in the same manner (fig. 138 A). The secondary laterals may branch again and this may be continued to the fourth degree, all the various branches lying in one plane. The ultimate branchlets, where they abut on others, cut off one or rarely two minute cells at their tips. These grow out into short haptera or tenacula (fig. 138 B, *h*) with a lobed apex which becomes firmly fixed to the other branch, and in this way the whole pinnate branch-system becomes firmly connected to form the blade. One species of *Struvea* is found in the tropical sponge *Halichondria* (212) ramifying through its substance in the form of irregularly branched threads and at certain points causing wart-like elevations where the normal stalked blades appear.

The long stalk of the monotypic *Chamaedoris* ((23), (24) p. 59, (28)) shows constrictions along its whole length and terminates in a rounded or cup-shaped structure (fig. 138 C) composed of numerous felted, irregularly branched threads with a single series of segments. At the apex of the primary stalk-like vesicle, where most of the contents accumulate, a series of usually three segments decreasing in size from below upwards is formed by segregative division (fig. 138 E). From each of these, as well as from the top of the stalk (fig. 138 F), a whorl of branches arises (cf. Dasycladaceae) which by their rich ramification give rise to the feltwork of the cup. The firmness of the felt is increased by the outgrowth from the filaments of short rhizoids (fig. 138 D, *h*) which at their expanded tips come into close contact with other threads.

The altogether tropical genus *Cladophoropsis* ((18), (24) p. 42, (172)) consists of much branched filaments, often showing unilateral ramification and exhibiting apical growth (fig. 139 A, B). The threads are twisted together to form cushions which are attached by rhizoids to rocks or other Algae, or lie as loose aegagropilous masses on the bottom. Cohesion of the filaments is brought about by means of occasional lobed haptera, formed at the ends of short side-branches or sometimes arising directly from the longitudinal walls of the cells (fig. 139 C, D). A characteristic feature of the genus is the usual absence of septa cutting off the branches at their base (cf. fig. 139 A, B). Early stages have not yet been studied, but the linear series of segments composing the mature plants are formed by segregative division (fig. 139 E, F), and

Fig. 137. *Siphonocladus*. A, *S. pusillus* (Kutz.) Hauck, young plant. B–I, *S. tropicus* (Crouan) J. Ag.; B, habit; C, branch arising from the cell (*a*), only the uppermost right-hand lateral has so far undergone segregative division; D, plasmolysed branch showing the separate segments; E, young plant; F, base of plant with septate rhizoids; G, zoosporangium; H, I, different stages of segregative division. *o*, apertures of zoosporangium; *r*, rhizoid; *s*, segments. (A after Schmitz; the rest after Boergesen.)

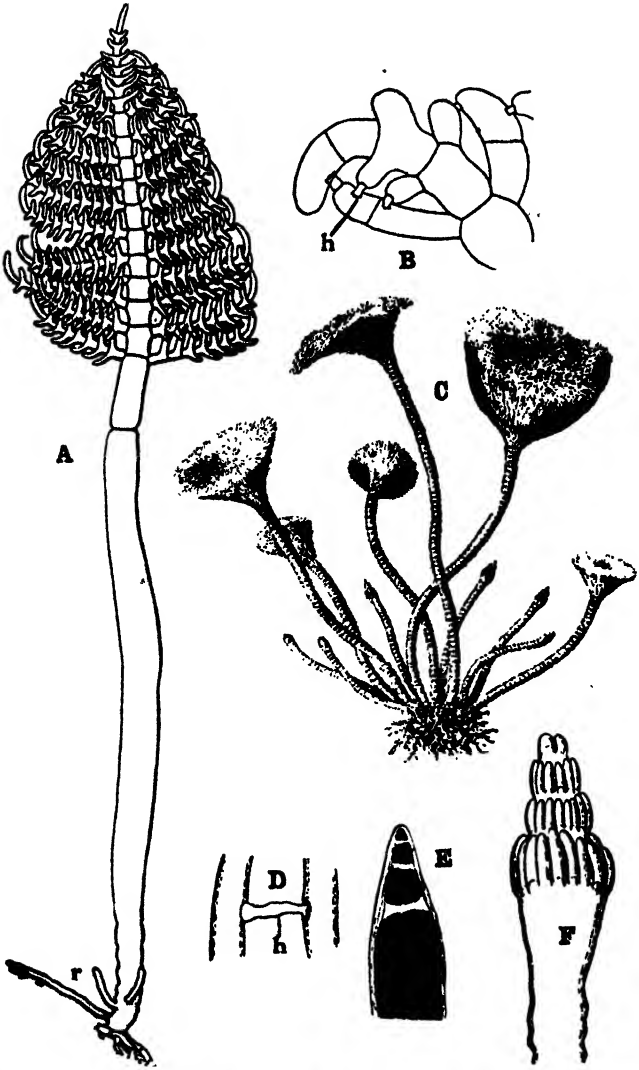

Fig. 138. *Struvea* and *Chamaedoris* (all after Boergesen). A, *Struvea elegans* Boerg., young plant. B, *S. anastomosans* (Harv.) Piccone, mode of connection of branches by tenacula (*h*). C–F, *Chamaedoris Peniculum* (Sol.) O. K.; C, habit; D, rhizoid-like hapteron (*h*) connecting two filaments; E, apex of young plant, protoplast recently divided; F, the same, formation of branches. *r*, rhizoid.

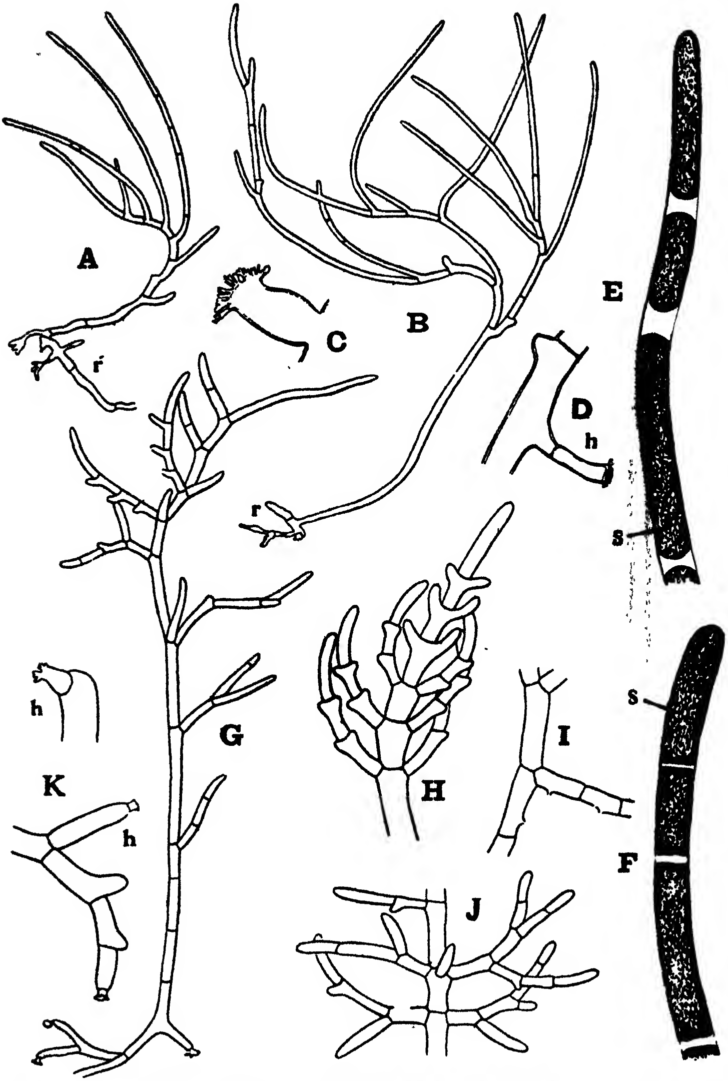

Fig. 139. *Cladophoropsis* and *Boodlea* (all after Boergesen). A–F, *Cladophoropsis membranacea* (Ag.) Boerg.; A, B, two specimens prepared out from a cushion; C, D, tenacula; E, F, apices of filaments showing segregative division. G–K, *Boodlea siamensis* Reinb.; G, part of thallus with basal rhizoids; H, J, threads with opposite branching; I, zoosporangia; K, summits of two branches with tenacula. *h*, tenaculum; *r*, rhizoid; *s*, segment.

the branches usually arise from them in the same way as in a *Siphonocladus*. Branches may, however, also originate from small lenticular cells cut off as in a *Valonia* ((24) p. 45).

A similar form is constituted by *Boodlea*,[1] but this is more copiously branched and often shows opposite or whorled arrangement of the laterals (fig. 139 G, H). The branches are joined to form a spongy cushion-like network by means of short haptera formed at their apices (fig. 139 K). In this genus septa are found at the bases of the branches. *Cladophoropsis* and *Boodlea* lack the annular constrictions of the forms previously described.

The genera *Microdictyon*[2] and *Anadyomene*[3] form small foliose expanses resulting from the abundant branching that occurs essentially in one plane. In the former the branches do not fit closely, so that they give rise to a rather regular and minute network in which the main threads stand out as more or less prominent veins, the whole resembling to a remarkable degree the skeleton of a dicotyledonous leaf (fig. 140 B). In *Anadyomene*, however, the branches are far more closely placed and in their entirety unite to form a usually continuous expanse (fig. 140 A). Both genera are mainly found in tropical seas, the species of *Microdictyon* usually inhabiting deep water; *M. Agardhianum* occurs in the Mediterranean. In both genera the lower segments of the thallus are produced into numerous, often thick-walled rhizoids which in their upper part are woven together to form a stalk (fig. 140 C).

In *Microdictyon* the branch-system consists of uniform cylindrical cells, those of the main axes only differing in size from the others. The ultimate branchlets grow vertically towards others, and at the points of contact become connected to them either by a thickened cellulose-ring (fig. 140 D) or by a tenaculum which is not cut off by a septum. In *Anadyomene* the main axes and their principal branches are composed of large club-shaped or cylindrical cells, while the wide interspaces between these are occupied by numerous pinnately arranged and closely aggregated unicellular laterals which are oval in shape (fig. 140 C) or sometimes lobed, the whole fitting together to form a uniform expanse. Where the branches abut on one another they are joined by cellulose-rings. The lobes of the smaller branches sometimes also grow at right angles to the general surface and may give the appearance of a definite cortex on either side of the main system (25).

The mode of division in the two genera just discussed has not yet been established. Boergesen ((25) p. 34) gives some details of branch-formation in a species of *Microdictyon* which he regards as affording evidence of segregative division, but this is not very strong. The two genera probably belong to the Valoniaceae, but their real affinities must remain unsettled until their detailed development has been studied.

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[1] See (24), (27), (31), (130), (215).

[2] See (13), (25) p. 27, (80), (172), (186).

[3] See (1), (25) p. 25, (80).

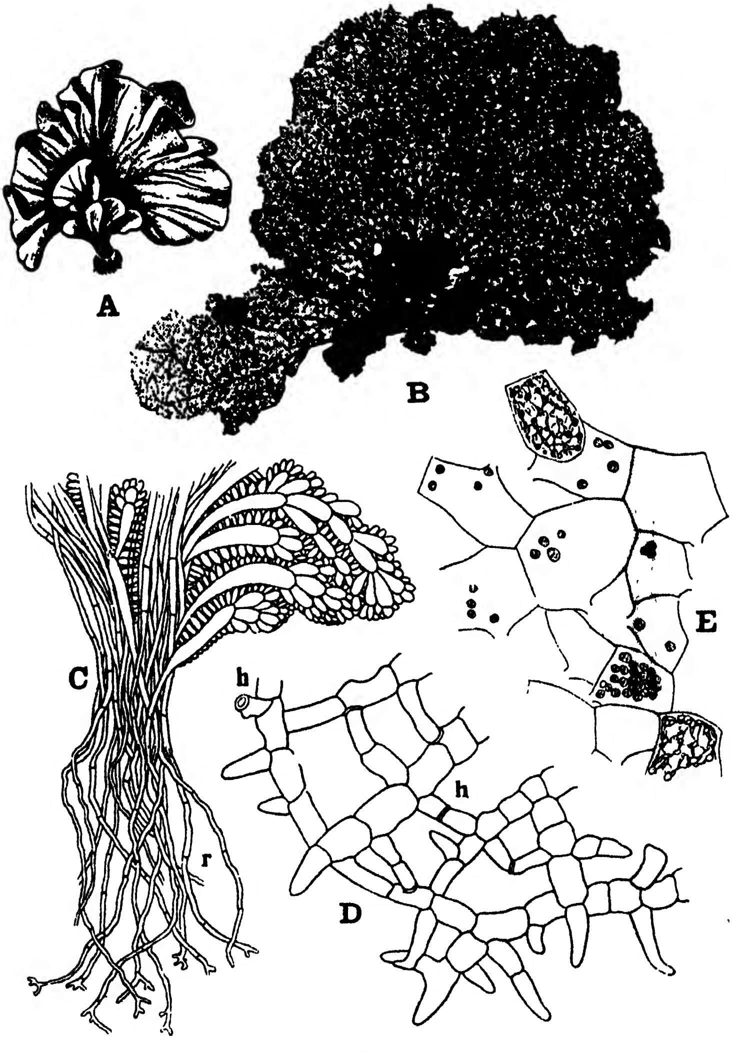

Fig. 140. *Microdictyon* and *Anadyomene*. A, C, *Anadyomene stellata* (Wulf) Ag.; A, habit; C, base of a plant. B, *Microdictyon Kraussii* J. E. Gray, habit. D, *M. Agardhianum* Decsne., part of thallus showing mode of connection of branches. E, *M. Calodictyon* (Mont.) Decsne., part of thallus with zoosporangia. *h*, haptera; *r*, rhizoids. (A after Kützing; B, D, after Setchell; C, E after Boergesen.)

The diverse genera included in Valoniaceae, in conformity with Printz (158), might equally well be referred to a number of separate families, as Boergesen (25) advocates. Thus, we have in the first place *Valonia* and *Dictyosphaeria*, closely related to *Halicystis* (p. 373), which Printz also classes in this family. *Ernodesmis*, *Siphonocladus*, *Struvea*, and *Chamaedoris* form another apparently natural group characterised by the annular constrictions on the main axes and sometimes also on the branches. *Cladophoropsis* and *Boodlea* are more definitely filamentous forms, while *Microdictyon* and *Anadyomene* are essentially distinguished by their habit. Should these two genera prove to belong here they would occupy the same relation to *Cladophoropsis* and *Boodlea* as *Struvea* does to *Siphonocladus*.

THE REPRODUCTION OF THE VALONIACEAE

Reproduction by swarmers is known in practically all cases. They are formed simultaneously in large numbers from the ordinary segments of the thallus (cf. figs. 135 F, 137 G, 140 E), and often most of these, apart from the rhizoids, may be involved. In *Anadyomene*, however, swarmers appear to be produced only in the smaller laterals. The swarmers are liberated from one (*Boodlea*, fig. 139 I; *Microdictyon*, fig. 140 E) or more (*Valonia*, *Dictyosphaeria*, *Cladophoropsis*, *Siphonocladus*, fig. 137 G, etc.) apertures which are sometimes situated at the ends of slightly protruded portions of the wall. They are mostly biflagellate (fig. 135 J), although four flagella have been reported in *Valonia* (113). Sexual fusion has so far not been observed, but Schussnig (182) records the occurrence of a reduction division prior to swarmer-formation in *V. utricularis*, so that it would seem that the swarmers of the Valoniaceae are gametes and that this family is diploid like other Siphonales.

In several cases (*Ernodesmis*, *Struvea*, cf. (24) p. 56) the protoplasmic contents of a segment have been found to divide into a number of rounded masses, which become enveloped by a membrane as in segregative division. These bodies appear to constitute cysts which give rise to new plants. Similar structures have been observed in *Valonia* and *Siphonocladus* ((24) p. 29, (134)). This suggests the possibility of regarding segregative division as a process of cyst-formation, in which the cysts develop *in situ*, instead of outside the parent plant. On this view the diverse members of the family would consist of colonial aggregates of coenocytic individuals resulting from retention of the reproductive units. Boergesen ((18) p. 265) has also compared the process to the formation of cysts in the gametangia of the Dasycladaceae.

(g) THE FAMILY CHAETOSIPHONACEAE

Wille (221) and Printz (158) include in the Valoniaceae the two simple genera, *Chaetosiphon* and *Blastophysa*, which combine a multinucleate organisation with the possession of hairs like those of the Chaetophoraceae. Some authorities (14, 97) have therefore referred them to the Chaetophorales, but the mere possession of hairs is scarcely sufficient to warrant this. *Chaetosiphon moniliformis* ((97) p. 338), only once observed as an endophyte in dead *Zostera* leaves in the Mediterranean, consists of a branched unseptate thread with occasional marked constrictions, the branches terminating in long unicellular hairs (fig. 141 A). The numerous chloroplasts assume the form of polygonal plates, very similar to those of Valoniaceae (fig. 141 B).

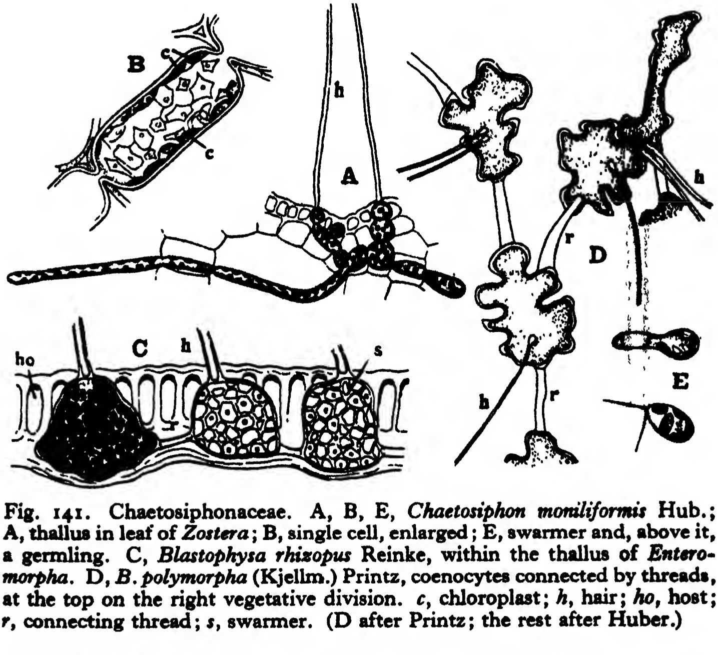

Fig. 141. Chaetosiphonaceae. A, B, E, *Chaetosiphon moniliformis* Hub.; A, thallus in leaf of *Zostera*; B, single cell, enlarged; E, swarmer and, above it, a germling. C, *Blastophysa rhizopus* Reinke, within the thallus of *Enteromorpha*. D, *B. polymorpha* (Kjellm.) Printz, coenocytes connected by threads, at the top on the right vegetative division. *c*, chloroplast; *h*, hair; *ho*, host; *r*, connecting thread; *s*, swarmer. (D after Printz; the rest after Huber.)

Blastophysa[1] occurs both epiphytic and endophytic in a number of marine Algae. The endophytic individuals are more or less rounded (fig. 141 C), while the epiphytes have the form of a lobed cushion with a thick membrane (fig. 141 D). Long delicate hairs (*h*), which are sometimes wanting, are borne singly or in groups. Multiplication is effected by narrow tubular outgrowths (*r*) which swell up at their tips to form a new coenocyte. This receives all the protoplasmic contents of the

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[1] See (22), (24), (97) p. 332, (157), (164), (180), (220).

outgrowth, the empty part subsequently becoming cut off (cf. *Chaetosphaeridium*, p. 287). Division of the coenocytes also occurs (164) and a detailed study of this process might shed some light on the affinities of the genus.

The zoospores are biflagellate in *Chaetosiphon* (fig. 141 E), quadriflagellate in *Blastophysa*. In the former they are produced in a part of the filament which becomes cut off by a septum and are stated to escape through the hairs which open at their tips. In *Blastophysa* they develop in the ordinary coenocytes (fig. 141 C) from which they are liberated through a kind of neck.

(*h*) THE FAMILY PHYLLOSIPHONACEAE

The commonest of these siphoneous endophytes is *Phyllosiphon*[1] which inhabits the intercellular spaces of the leaves and petioles of various Araceae, mostly in the Tropics, although *P. Arisari* Kühn occurs in *Arisarum vulgare* in Europe.[2] Another genus, *Ostreobium* (29, 157), is found in the old shells of marine Molluscs (oysters, etc.), not uncommonly together with *Gomontia polyrhiza* or in the calcareous substance of Corals. The richly branched threads of *Phyllosiphon* (fig. 142 E) do not penetrate the host's cells, but those surrounding the intercellular spaces occupied by the alga are stimulated to abundant division, so that gall-like swellings are produced (fig. 142 A); ultimately the adjacent cells are killed, so that the presence of the endophyte also makes itself noticeable by the appearance of discoloured patches. The threads possess numerous nuclei, those at the colourless growing tips being relatively large, whilst in the older parts they are smaller as a result of repeated division. The threads also contain pale discoid chloroplasts, and according to Nicolas (138) *Phyllosiphon* is capable of photosynthesis from the time of spore-formation onwards. *Ostreobium* has a similar well-branched filamentous thallus in which a certain amount of anastomosis occurs between the branches and occasional septa are formed.

Weber van Bosse's *Phytophysa* (215) produces yellow or dark-coloured galls on the surface of the vegetative organs of *Pilea* (Urticaceae) (fig. 142 B). These contain large pear-shaped coenocytes with numerous chloroplasts (fig. 142 G, *a*). This genus might with almost equal justice be referred to the Chlorochytrieae (cf. (147) p. 492), with which the Phyllosiphonaceae altogether have something in common.

Reproduction is in all cases effected by oval aplanospores which are formed in great profusion. In *Phyllosiphon* (fig. 142 C) they are produced throughout large parts of the thallus and when mature con-

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[1] See (32), (107), (114), (119), (175), (206).

[2] A species of *Phyllosiphon* has been found in Scotland by Prof. J. M. F. Drummond.

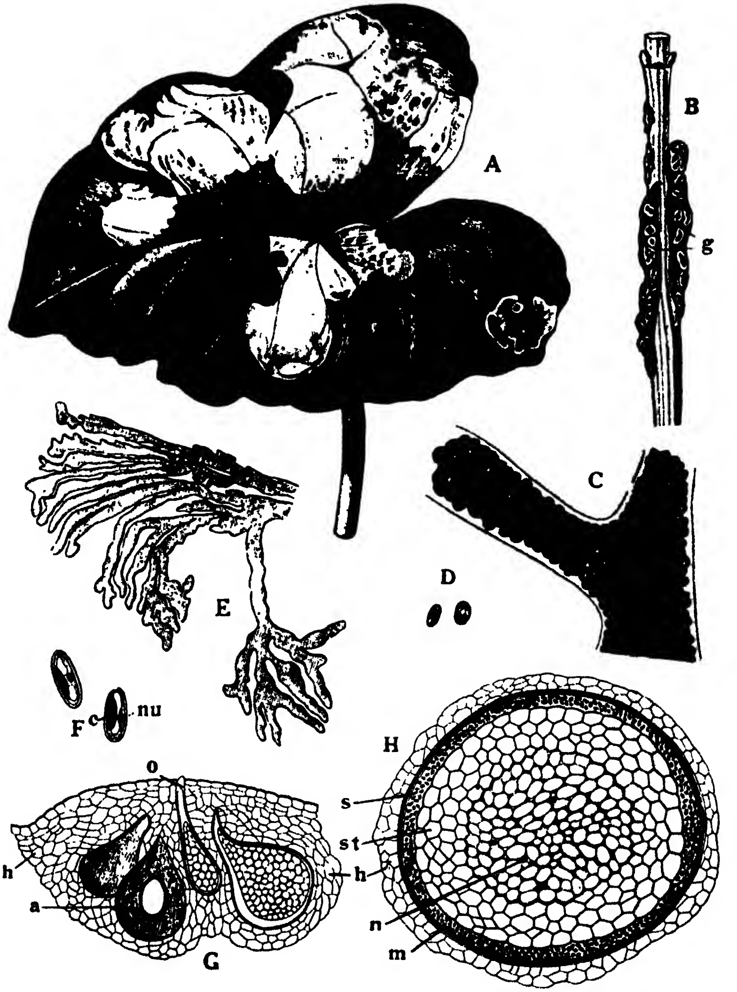

Fig. 142. Phyllosiphonaceae. A, C–E, *Phyllosiphon Arisari* Kühn; A, diseased leaf of *Arisarum vulgare*, the white areas due to the alga; C, part of a thread with spores; D, spores; E, branched threads from petiole of host. B, F–H, *Phytophysa Treubii* van Bosse; B, stem of *Pilea*, with galls (*g*) due to the alga; F, aplanospores; G, section of a gall; H, section of alga at time of spore-formation. *a*, endophyte (in G); *c*, chloroplast; *h*, host; *m*, membrane; *n*, central protoplasm of spore-forming stage (in H); *nu*, nucleus; *o*, tubular penetration of alga (in G); *s*, spores; *st*, sterile cells (in H). (A, C–E after Just; the rest after Weber van Bosse.)

tain a single nucleus and chloroplast (fig. 142 D). The threads possess a double membrane, the inner arising later than the outer. When the spores are mature, the outer membrane ruptures below a stoma, while the inner absorbs moisture and swells; pressure is thus exerted on the mass of spores which are extruded as a fine mucilaginous spray through the stoma. In *Ostreobium* the spores are formed in the clavate tips of the threads. In *Phytophysa* (fig. 142 H) the peripheral protoplasm of the coenocyte becomes denser and alone forms the spores (*s*); between it and the central protoplasm (*n*) several layers of sterile polygonal cells (*st*) with cellulose walls are formed. The spores (fig. 142 F) are liberated in mucilage by rupture of the membrane of the coenocyte and of the overlying tissue of the host.

The spores give rise to a thread which, in *Phyllosiphon*, penetrates the host either through a stoma or between two epidermal cells. The young threads contain very little chlorophyll and are probably parasitic, while the pale colour of the chloroplasts even in the mature threads speaks for a diminished assimilatory activity. The extent of the parasitism can, however, with our present knowledge scarcely be assessed. *Phytophysa* behaves like a *Chlorochytrium*, the tip of the outgrowth from the spore swelling to form the coenocyte which then becomes cut off from the empty part behind (cf. fig. 142 G, *o*). Possibly *Phyllosiphon* is the only truly siphoneous member of this family.

(*i*) THE FAMILY VAUCHERIACEAE

VEGETATIVE STRUCTURE

The oogamous Vaucheriaceae occupy an isolated position with reference to the remaining families of Siphonales. They comprise the widely distributed *Vaucheria* (78, 88, 89, 211) and the monotypic *Dichotomosiphon*, established by Ernst (59) in 1902 and apparently commoner in America than in Europe. Heering ((89) p. 96) has added a further genus *Vaucheriopsis* for a species of *Vaucheria* (*V. arrhyncha* Heidinger, (90) p. 331) that differs in several respects from the others and approaches *Dichotomosiphon*, whilst Yamada's *Pseudodichotomosiphon* ((231*b*) p. 83, first described as *Vaucheria constricta* (231*a*) p. 110) combines certain characteristics of *Dichotomosiphon* and *Vaucheria*. The Vaucheriaceae are most widely distributed in temperate regions.

The species of *Vaucheria* usually occur in situations where there is good aeration, i.e. where they are subject to the splashing or trickling of water, or in streams, but a number inhabit damp ground (e.g. *V. sessilis*, *V. hamata*) and a few occur in the tidal zone or in the sublittoral region (e.g. *V. piloboloides*). *V. Thureti* Woron. is common on mud or mud admixed with sand in the littoral region ((37) p. 64), while this and a number of other species are frequent on salt-marshes (32a). The diverse species nearly always appear as a felt of monopodially branched, rather coarse filaments with apical growth, although upright tufts, often showing marked positive phototropism, arise from the basal weft in some forms. The threads commonly develop incrustations of carbonate of lime, and very striking examples have been observed in *V. Debaryana* (111).

Dichotomosiphon is aquatic and Smith ((188a) p. 273) mentions records of its occurrence in deep water. The threads of this alga grow erect (fig. 144 A) and, in their dichotomous branching with marked constrictions associated with local yellow- or brown-coloured thickenings of the membrane just above the points of branching (fig. 144 B), resemble to a very marked extent the threads of the Codiaceae. The thickenings are by no means restricted to the points of branching, sometimes occurring at regular intervals along the threads. In older plants tri- and tetrachotomy is found, as well as a certain amount of lateral branching. The threads of *Dichotomosiphon* arise from colourless branched rhizoids which ramify in the substratum, while the young threads of the *Vaucherias* are usually attached by a lobed hapteron (fig. 144 J). *Pseudodichotomosiphon* resembles *Dichotomosiphon* in habit. According to Ernst (59) and Virieux (207) both membranes and thickenings of *Dichotomosiphon* are composed of cellulose, whilst Mirande (124) and Puymaly (160) state that they consist of callose and pectic substances. In *Vaucheria* (124, 230) the cellulose is associated with pectic substances. The membrane is relatively thin, but thicker in the terrestrial than in the aquatic forms.

The cell-contents show the usual siphoneous distribution, but the numerous discoid chloroplasts always lack pyrenoids. According to Senn ((185) pp. 4, 36) those of a *Vaucheria* assume a spherical form in intense light, while they are able to change their position when exposed to one-sided illumination. In *Vaucheria*, where no starch is normally formed, the excess assimilates are stored in the form of oil (30), countless drops of which are found in the cytoplasm; according to Meyer (121) this is not a true fat. Tiffany (204) states that, if *Vaucheria* is grown under constant illumination, the food-reserves become partially or entirely starch. In *Dichotomosiphon* large starch-grains are formed in all the green parts (cf. p. 68), while Ernst ((59) p. 125) suspects an origin from leucoplasts in the colourless rhizoids (cf. also (43) p. 201). In *Vaucheriopsis* ((90) p. 331) there is no oil, its place being taken by food-reserves of unknown nature. Molisch (125) records spindle-shaped protein-bodies in the cell-sap of a *Vaucheria*.

The nuclei of *Vaucheria* have been studied especially by Kurssanow (115) and Hanatschek (85), both of whom record centrosomes and an annular arrangement of the chromosomes during nuclear division (fig. 10 S–U, p. 70).

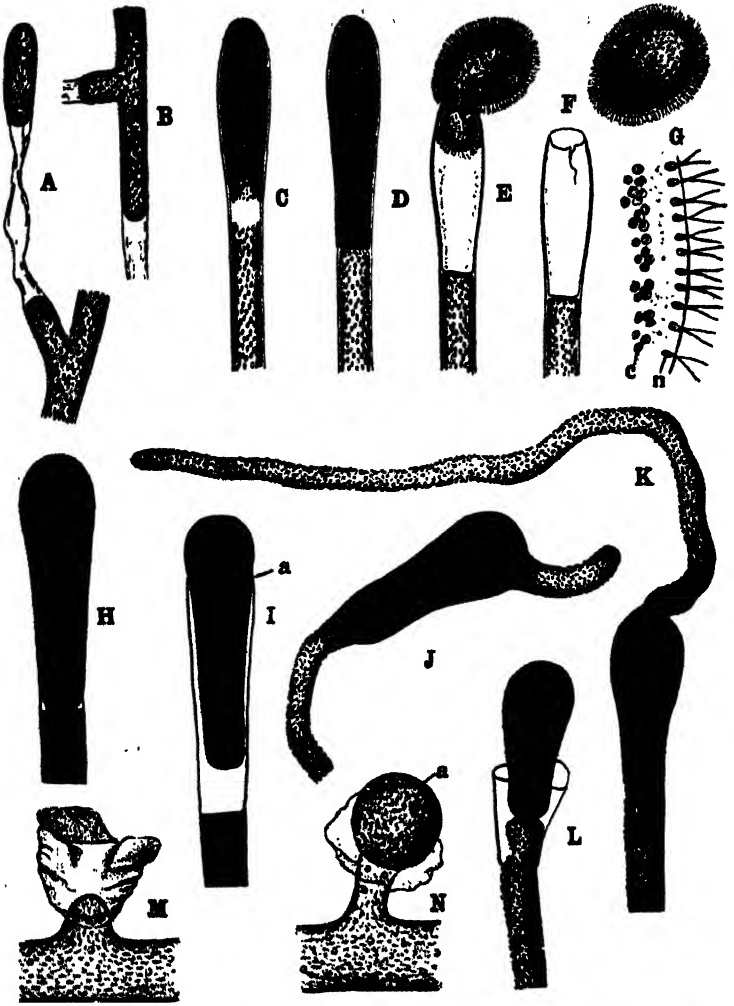

Fig. 143. Asexual reproduction of *Vaucheria*. A, B, *Vaucheria* sp., formation of septa in injured thalli. C–G, *V. repens* Hass.; C–F, formation and liberation of zoospore; G, part of periphery of latter. H–L, *V. piloboloides* Thur.; H, formation and I, liberation of aplanospore; J, K, direct germination of sporangium; L, proliferation of thread into dehisced sporangium, pushing aplanospore in front of it. M, N, *V. uncinata* Kütz., formation and liberation of aplanospore. *a*, aplanospore; *c*, chloroplasts; *n*, nuclei. (A, B after West; G after Strasburger; H–L after Ernst; the rest after Goetz.)

Injury to the thallus of a *Vaucheria* results in the formation of a septum (fig. 143 A, B) cutting off the injured part (86, 124); otherwise septa are rarely formed except in connection with reproduction.

ASEXUAL REPRODUCTION

Apart from abundant vegetative multiplication by means of detached fragments, prolific asexual reproduction of *Vaucheria* is effected by the familiar multiflagellate zoospores.[1] These are produced singly in club-shaped sporangia which are cut off from the somewhat swollen ends of branches. Into these large numbers of chloroplasts and nuclei stream so that the central vacuole diminishes in size and the tips appear deep green (fig. 143 C).

At the base of the developing sporangium a transverse bridge of colourless cytoplasm appears which breaks across its middle (fig. 143 C), after which the two severed protoplasts contract and separate slightly. The intervening space is stated to be occupied by sap continuous with that enveloped by the two protoplasmic masses whose edges show constant changes of shape. A few minutes later the two masses again approach each other and, as this happens, their free edges bend in and unite to form a complete plasma envelope, cutting off the respective sap-vacuoles from one another. When the surfaces of the protoplasts meet, each secretes a delicate membrane, so that the sporangium becomes cut off by a septum composed of two layers (fig. 143 D, E). There is an indication here of segregative division.

Within the sporangium an inversion of the relative positions of chloroplasts and nuclei ensues, so that the latter come to lie peripherally within the colourless surface protoplasm (fig. 143 G), and this is followed by contraction of the contents and the protrusion of a pair of short equal flagella opposite each nucleus. By gelatinisation of the membrane at the apex a narrow aperture is formed through which the large oval or pyriform zoospore pushes its way (fig. 143 E, F). Sometimes the part first protruded becomes separated from that still left in the sporangium and two zoospores are formed instead of one.

The zoospore includes the central sap-vacuole of the original sporangium which may even be traversed by strands of cytoplasm, and this, quite apart from the paired disposition of the flagella opposite the nuclei, indicates that the zoospore is to be regarded as a compound structure representing a number of biflagellate zoospores which have failed to separate. In *V. ornithocephala* Ag. the flagella are densely aggregated only at the anterior pole, whilst elsewhere they are sparsely scattered (78).

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[1] See (12) p. 291, (108) p. 3, (199) p. 84.

Not all species of *Vaucheria*, however, produce zoospores. Aplanospores, formed when the plants are exposed to drought, constitute the normal means of asexual reproduction in a number of species. In *V. geminata* (225) and *V. uncinata* ((78), (108) p. 90, (211)) the aplanosporangia, which usually arise at the ends of short laterals, possess a more or less rounded form, and the spores enveloped in a thin membrane merely drop out of the sporangium after the wall of the latter has torn open irregularly (fig. 143 M, N).

In *V. piloboloides* (227), on the other hand, the aplanosporangia resemble the ordinary zoosporangia in form and position and liberate the elongate aplanospores in the same way through a narrow apical aperture (fig. 143 H, I). According to Ernst ((61) p. 370) the aplanospore enlarges considerably during liberation, while a slight contraction of the empty sporangium-membrane is evident. It seems probable that a considerable osmotic pressure is realised within the intact aplanosporangium and that this leads to its apical rupture, with the subsequent contraction of the membrane. *V. piloboloides* serves to connect the normal mode of multiplication by zoospores with the special type of aplanospore-formation met with in *V. uncinata*, etc. In the former species the aplanospores have been observed to germinate within the sporangium, or the whole sporangium without contraction of its contents may grow out into a new thread (fig. 143 J, K).

In *Dichotomosiphon* (59) no zoospores are formed, their place being taken by somewhat irregular club-shaped akinetes (gemmae) formed at the ends of special thin rhizoid-like branches (fig. 144 C) and separated from the empty part behind by a thick brown septum (*s*). These structures may well be equivalent to an entire aplanosporangium of *V. piloboloides*. A somewhat similar formation of akinetes has been recorded in *V. megaspora* Iwanoff (99), where they arise at the ends of short lateral branches which receive all the protoplasmic contents of the adjacent parts of the thread before becoming cut off by a septum. They sometimes germinate *in situ*.

The zoospores of *Vaucheria* generally escape in the morning or after the plants have been in darkness. According to Klebs (108) they can always be obtained if filaments kept moist for some days are soaked in water or removed from a dilute nutritive solution into pure water or transferred from running to still water. The zoospores are sluggish in their movements which continue only for about fifteen minutes. On coming to rest the flagella are withdrawn and a thin membrane is secreted; germination follows almost immediately by the protrusion of one or two tubular outgrowths, one of which usually attaches itself to some substratum by a colourless lobed holdfast (fig. 144 H–J). The akinetes of *Dichotomosiphon*, which can pass through a resting period, germinate in the same way.

Stahl (193) and Puymaly (161) have observed in terrestrial forms of *Vaucheria geminata* and *V. hamata*, probably in response to drought, a septation of dichotomously branched filaments into a series of segments separated by thick gelatinous transverse walls, the segments being replete with oil (fig. 144 F). The cysts thus formed may remain connected for a time by the membrane of the parent-filament, con-

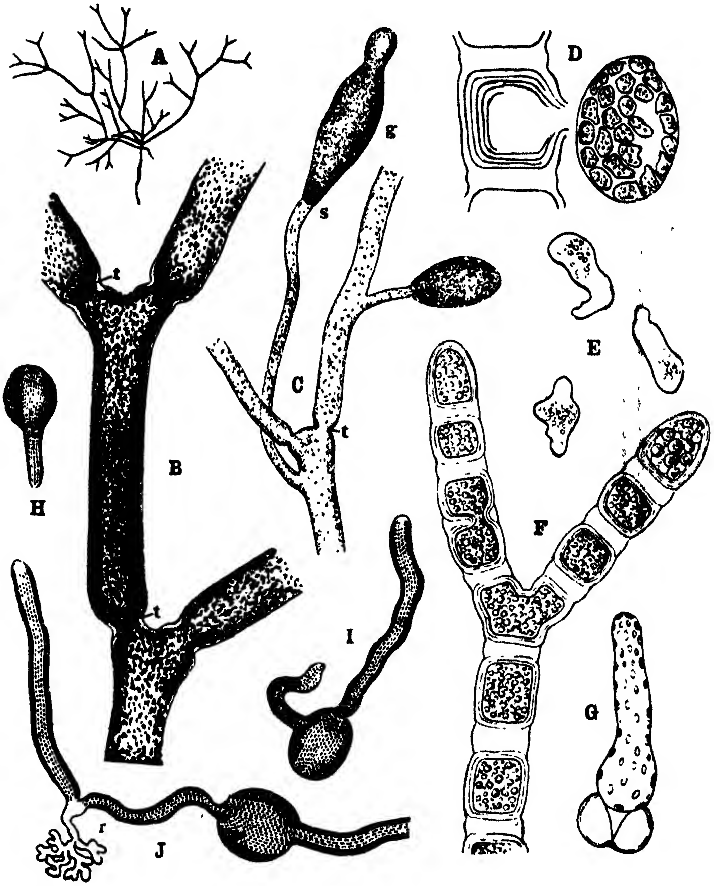

Fig. 144. A–C, *Dichotomosiphon tuberosus* (A. Br.) Ernst (after Ernst); A, young plant; B, part of a thread; C, thread with two akinetes (*g*). D–G, *Vaucheria geminata* DC. (after Stahl); F, *Gongrosira*-stage, with thick-walled akinetes; D, liberation of contents; E, three amoebae; G, germinating cyst. H–J, *V. sessilis* (Vauch.) DC. (after Sachs), stages in germination of zoospore. *r*, rhizoid; *s*, septum; *t*, membrane-thickenings.

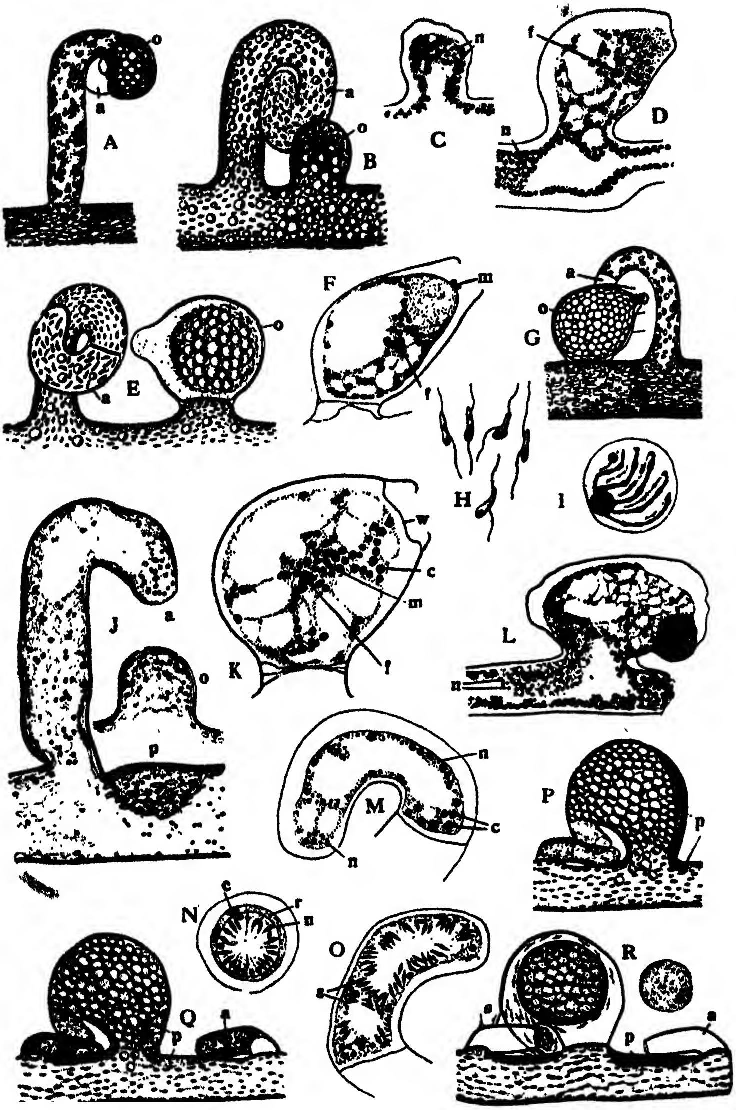

Fig. 145. Sexual reproduction of *Vaucheria*. A, *V. hamata* (Vauch.) Lyngb.; B–G, I–K, M–O, *V. sessilis* (Vauch.) DC.; H, *V. synandra* Woron.; L, *V. pachyderma* Walz; P–R, *V. aversa* Hass. A, oospore in oogonium,

stituting the so-called *Gongrosira*-stages. The cysts either grow direct into a new thread (fig. 144 G) or, when they are approaching maturity, can divide to form a number of small masses which are liberated as amoebae (fig. 144 D, E) and which likewise subsequently give rise to new individuals.

SEXUAL REPRODUCTION

The ordinary method of preparing for a resting period is by the production of oospores which is of frequent occurrence in nature. The majority of the members of the family are monoecious, but the large *Vaucheria dichotoma* is dioecious. In *Vaucheria* the antheridia and oogonia usually arise close together at intervals along the threads (fig. 145 B, E), but in some species (*V. terrestris* Lyngb., *V. geminata*) they are found on special side-branches with a terminal antheridium and a number of lateral oogonia (fig. 145 A).[1] There is, however, considerable diversity of arrangement, even in different individuals of the same species. The development of the sexual organs has been studied in a considerable number of species.[2] Regarding the conditions of formation of sex organs, see (108), (126).

The oogonia in *Vaucheria* usually appear as sessile or very shortly stalked lateral outgrowths. They soon assume a more or less rounded form (fig. 145 B, C) and ultimately (sometimes only just before fertilisation, cf. (38), (128)) become cut off by a septum near the base which according to Davis (44) and Oltmanns (145) is formed in just the same way as that cutting off the zoosporangium. At this stage (fig. 145 E, P, R) the oogonium is densely filled with oil and chloroplasts, but contains only a single central nucleus which gradually acquires quite considerable dimensions (fig. 145 D, *f*). According to Mundie (128) one or two periods of nuclear division are recognisable

[1] Under certain conditions such sexual branches can develop into vegetative threads of unlimited growth and the same change may take place in young developing oogonia (47, 72, 137, 219).

[2] See (38), (44), (90), (128), (145), (155), (223).

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antheridium dehisced; B, young sex organs; C, young oogonium stained to show nuclei; D, later stage, nuclei (*n*) returning to main thread; E, sex organs, oogonium shortly before aperture is formed; F, K, two stages in fertilisation; G, oogonium at fertilisation stage; H, spermatozoids; I, nucleus of zygote in synapsis; J, young sex organs; L, young oogonium, nuclei (*n*) returning to main thread; M, O, development of antheridium; N, transverse section of same; P, Q, successive stages in development of oogonium, showing movement of the special cytoplasmic mass (*p*) with the supernumerary nuclei; R, fertilisation. *a*, antheridium; *c*, chloroplasts; *f*, female and *m*, male nucleus; *n*, nuclei; *o*, oogonium; *p*, special cytoplasmic mass of oogonium; *r* (in N), residual cytoplasm; *s*, spermatozoids; *w*, membrane over oogonial aperture. (A, G after West; H after Woronin; I after Hanatschek; J, P–R after Couch; L after Heidinger; the rest after Oltmanns.)

in the developing oogonium, which is denied by Williams. The uninucleate condition is in all probability attained by all but one of the nuclei returning to the main filament (38, 90, 145) (fig. 145 D, L), although Davis (44) believed he had established that it arose by degeneration of all but one and this has been reaffirmed by Williams (223). Couch (38) has demonstrated the former condition very clearly for a number of species and has traced the movement of a special mass of cytoplasm containing the supernumerary nuclei from the oogonium back into the main thread (fig. 145 P, Q, R, *p*).

The maturation of the oogonium is marked by the development of a usually one-sided beak (fig. 145 D, E, L), the tip of which gelatinises and forms an aperture opposite to which lies the colourless receptive cytoplasm of the ovum, part of which is extruded in the form of a sphere (fig. 145 G, R). Thereupon the chloroplasts and oil-drops take up a central position (always?) leaving a clear superficial lining layer (fig. 145 E), while the whole ovum contracts more or less markedly as a result of the extrusion of sap from the central vacuole. In *V. dichotoma* (190) the spherical oogonia have the aperture situated apically (fig. 146 F), while in some of the marine species (e.g. *V. coronata* Nordst.) the oogonia develop several apertures.

In *Vaucheriopsis* (90), where the sexual organs are borne on short lateral branches, the oogonia do not develop a beak and their membrane breaks open irregularly at maturity, so that the ovum is held loosely within the open female organ (fig. 146 D). *Dichotomosiphon* (59) produces its sexual organs at the ends of terminal forking branchlets of the main threads, each oogonium and antheridium being situated on a separate branch (fig. 146 B); after fertilisation the thread below the sex organ can carry on vegetative growth. There is no contraction of the ovum which from the first contains hardly any vacuole; the septum is formed only just prior to fertilisation. In neither genus is there any extrusion of cytoplasm from the receptive spot. *Pseudodichotomosiphon* (231 *b*) resembles *Vaucheria* in having the sex organs arranged along the sides of the threads.

The antheridia of *Vaucheria*, which mostly develop simultaneously with the adjacent oogonia (fig. 145 B), commonly appear as strongly curved cylindrical tubes which become cut off from the thread by one or by two septa, usually situated rather high up in the tube (cf. fig. 145 E, G). The nuclei within the young antheridium (fig. 145 M) undergo further subdivision (not in *V. geminata* according to Williams), and ultimately a small mass of cytoplasm becomes appropriated to each to constitute a spermatozoid. In the mature antheridium of *V. sessilis* the spindle-shaped spermatozoids form a radially arranged group between the central vacuole and the unused peripheral cytoplasm (*r*) containing the chloroplasts (fig. 145 N, O). It seems that in other species there are differences in detail, as Oltmanns ((146) p. 424) points out. In particular it should be noted that the mature antheridia of many species (*V. piloboloides*, *V. Thureti*, etc. (227)) are quite colourless. Opening of the antheridia usually takes place by a single apical aperture (fig. 145 R), but in *V. Debaryana* (228) and others there are several apertures (fig. 146 C). Some of the waste cytoplasm is usually extruded with the sperms. The antheridia show considerable differences in form and mode of opening and the classification of the species is mainly based on these features.

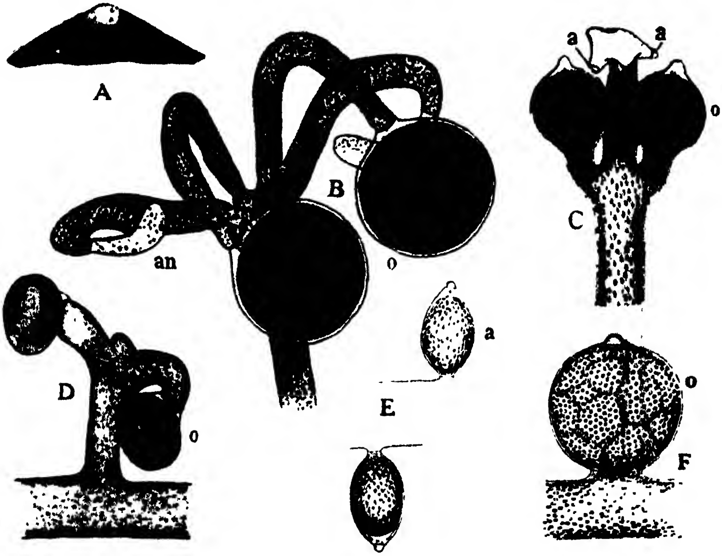

Fig. 146. A, B, *Dichotomosiphon tuberosus* (A. Br.) Ernst (after Ernst); A, apex of oogonium after fertilisation; B, group of oogonia and antheridia. C, *Vaucheria Debaryana* Woron. (after Woronin). D, *Vaucheriopsis arrhyncha* (Heid.) Heering (after Heidinger), oogonia at time of fertilisation. E, F, *Vaucheria dichotoma* Ag. (after Walz); E, antheridia; F, oogonium. *a*, aperture of antheridium; *an*, antheridium; *o*, oogonium.

The male cells are exceedingly minute, oval or pear-shaped, and quite colourless; they are provided with two laterally inserted flagella, one pointing forwards and the other backwards (cf. fig. 145 H). In many cases probably the adjacent oogonium is fertilised, but there is probably no truth in older accounts, recently revived by Mundie, that there is any direct fusion between the antheridium and the receptive portion of the oogonium.

After fertilisation in *Vaucheria* a membrane first forms across the oogonial aperture (fig. 145 K, *w*), and subsequent to this the thick several-layered envelope of the zygote (fig. 145 A) is secreted. At the same time the oil-drops unite to form a small number of central globules, while the chloroplasts disappear or at least become unrecognisable. In most cases the central cytoplasm of the oospore contains a number of reddish or brownish bodies which are regarded as degeneration products of the chlorophyll. Both in *Vaucheriopsis* and *Dichotomosiphon*, however, the oospores retain a normal green colour and only develop a relatively thin envelope. Those of the latter remain enclosed within the oogonia which do not become detached from the parent threads. The oospores, after a resting period, always germinate direct. Wettstein (218) has caused artificial parthenogenesis in *V. hamata* by pricking the mature oogonia.

The investigations of Hanatschek (85), though not absolutely convincing, make it highly probable that reduction occurs in the first nuclear division in the germinating oospore of *Vaucheria*; the only decisive stage seen was that of synapsis (fig. 145 I). Mundie (128) had previously affirmed that reduction took place in the maturing oogonium, but the evidence produced in support of this view is altogether inconclusive. It remains to be seen whether *Dichotomosiphon* is likewise haploid.

THE AFFINITIES OF THE VAUCHERIACEAE

The exact relationship of the four genera included in the Vaucheriaceae is still uncertain. There is so much resemblance between the sexual organs that it is difficult to believe that the forms here grouped together have not arisen from a common ancestry. Nevertheless, in view of the very marked parallelism that the researches of the last twenty years have displayed between algal forms of quite different affinities, such a possibility must not be dismissed. That *Dichotomosiphon* belongs to the Siphonales can hardly be doubted in view of its metabolism and the marked resemblance to Codiaceae in the vegetative characters. It is *Vaucheria* that is under suspicion, and it cannot be denied that some of its characters point rather to Xanthophyceae (Heterokontae) than to Siphonales. These characters are the stated presence of more xanthophyll than usual in the chloroplasts ((16), (158) p. 328), the usual storage of oil and absence of starch, and the mode of arrangement of the flagella on the spermatozoids, although in this last respect there is not much resemblance to the true Xanthophycean type. Pascher (see (89) p. 69, footnote) further expresses doubts as to the equality of the pairs of flagella on the zoospores. In how far *Vaucheriopsis* shows features, apart from the nature of its food-reserves, that would separate it from *Vaucheria* is at present not clear.

In some respects (e.g. the behaviour of the oospore) it certainly helps to link the latter genus with *Dichotomosiphon*.

It cannot be questioned that the development of the reproductive cells exhibits many points of analogy with the Oomycetes (cf. (44), (223)). Thus, the compound zoospore of *Vaucheria*, like the gonidium of various Peronosporaceae, no doubt represents the contents of an entire sporangium, and the resemblance is even more marked where substitution of aplanospores has taken place. The akinetes of *Dichotomosiphon* afford another parallel. There are also similarities in the detailed structure of the sex organs. How far such resemblances are indicative of real affinities and how far they may be the result of convergent development against a siphoneous background it is at present impossible to say.

Printz ((158) p. 252) and others regard the Monoblepharidaceae as colourless members of the Siphonales. Possibly *Allomyces*[1] should be treated in the same way.

TAXONOMY

The following is a synopsis of the classification of Siphonales here adopted, the grounds for which have been given in full in the preceding pages.

1. *Protosiphonaceae:* Follicularia, Halicystis, Protosiphon, Sphaerosiphon.
2. *Caulerpaceae:* Bryopsis, Caulerpa, Pseudobryopsis.
3. *Derbesiaceae:* Derbesia.
4. *Dasycladaceae:* Acetabularia, Acicularia, Batophora, Bornetella, Coelosphaeridium, Cymopolia, Dactylopora, Dasycladus, Digitella, Diplopora, Gyroporella, Halicoryne, Mizzia, Neomeris, Palaeodasycladus, Primicorallina, Rhabdoporella, Thyrsoporella, Triploporella, Vermiporella.
5. *Codiaceae:* Avrainvillea, Boodleopsis, Boueïna, Codium, Dimorphosiphon, Halimeda, Ovulites, Palaeoporella, Penicillus, Pseudocodium, Rhipidodesmis, Rhipilia, Rhipocephalus, Udotea (including Flabellaria).
6. *Valoniaceae:* Anadyomene, Boodlea, Chamaedoris, Cladophoropsis, Dictyosphaeria, Ernodesmis, Microdictyon, Siphonocladus, Struvea, Valonia.
7. *Chaetosiphonaceae:* Blastophysa, Chaetosiphon.
8. *Phyllosiphonaceae:* Ostreobium, Phyllosiphon, Phytophysa.
9. *Vaucheriaceae:* Dichotomosiphon, Pseudodichotomosiphon, Vaucheria, Vaucheriopsis.

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[1] See Kniep, in *Ber. Deutsch. Bot. Ges.* **47**, 199–212, 1929; *Zeitschr. Bot.* **22**, 433–41, 1930.

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Order IX. *CHARALES*

The Charales stand considerably apart from other Chlorophyceae in the complexity of their sexual reproductive organs, the occurrence of a protonemal stage in the development of the zygote, and in certain features of their vegetative organisation. For these reasons many (1, 30, 47, 62) have regarded them as representing not only a distinct class, but even a distinct division of the lower plants, whilst some (6, 13, 78) have suggested a transference to the Bryophyta. These points of view are discussed on p. 465, but it may be emphasised here that the Charales are haploid like so many other Chlorophyceae and like all the known oogamous forms and that, in vegetative organisation at least, considerable parallels are to be found in other Green Algae (cf. *Draparnaldiopsis*, p. 254). The sex organs, and in particular the antheridium, though quite unparalleled among the Algae, are equally unique when considered in relation to other groups of plants.

The members of the only family, the Characeae, are widely distributed in waters which are not subject to too much movement and which afford the sandy or muddy substratum in which the anchoring rhizoids can find a suitable foothold; some species are confined to fresh, others to salt water (*Chara baltica*), whilst yet others occur in both habitats (87). They are able to exist with a small supply of oxygen (42) and can thrive where the substratum contains much decomposing matter (frequently including H_2S, cf. (87)); on the other hand they require pure water and are scarcely to be found in water liable to become turbid or where there is any contamination (30). They usually form extensive subaquatic meadows and in larger bodies of water constitute characteristic zones extending to a considerable depth in clear water, *Nitella* in general going deeper than *Chara* (30, 58, 67). The abundant incrustation with carbonate of lime that characterises most species of the latter genus often leads to the accumulation of considerable calcareous deposits ((30) p. 11). The presence of calcium is essential (81), although the demands of the different species vary (87).

The frequent avoidance of waters harbouring Characeae by Mosquito-larvae has occasionally led to the expression of the view that they excrete substances having larvicidal properties, but for this opinion there is at present at least no clear foundation (9, 10, 31, 88).

VEGETATIVE STRUCTURE[1]

All the members of the family exhibit a whorled arrangement of the laterals of limited growth that gives the plants an equisetoid habit

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[1] See (22), (23), (26), (30), (33), (41), (47), (65), (72).

(fig. 147). The laterals (often spoken of as "leaves") arise from special nodes consisting of a transverse layer of cells, while the elongate internodes are composed of a single cell which is, however, corticated in *Chara* and its allies. The plants are practically always erect and commonly grow to a height of about 20–30 cm., but some (e.g. *Nitella batrachosperma*, fig. 147 C) are much smaller, while at the other extreme *Nitella cernua* A. Br., an inhabitant of Tropical America, may attain to a metre or more in height, with internodal cells reaching a length of 25 cm. The shoots are negatively geotropic and positively phototropic, and growth-curvatures in response to stimuli take place in the still growing internodes (63).

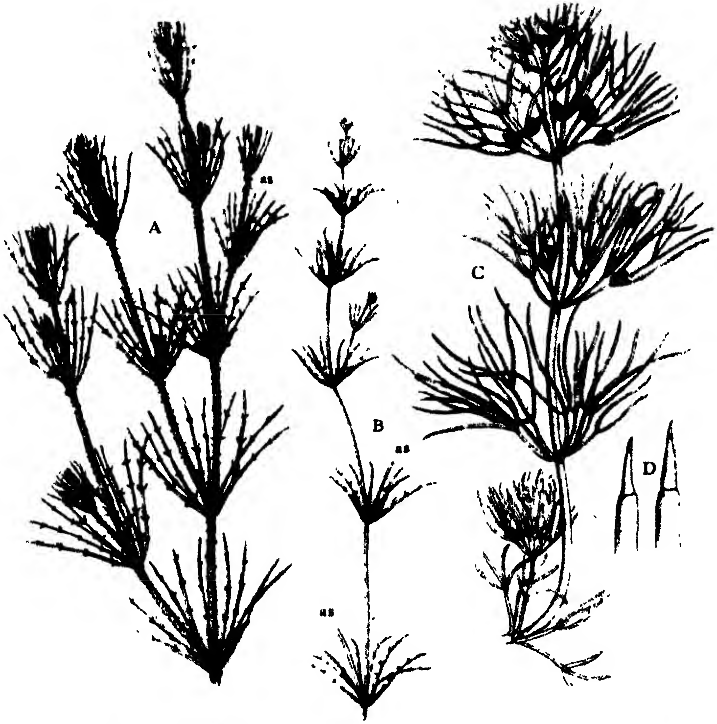

Fig. 147. Habits of diverse Characeae (all after Groves & Bullock-Webster). A, *Chara hispida* L. B, *C. vulgaris* L. C, D, *Nitella batrachosperma* (Reichenb.) A. Br.; D, apices of ultimate branches. *as*, axillary (long) shoots.

Growth is in all cases effected by a dome-shaped apical cell (fig. 148 A, *m*), cutting off a single series of segments (*s*) parallel to its flat base. Each segment divides into a biconcave upper (*n*) and a biconvex lower half (*i*), of which the former gives rise to a node and the latter to an internode (cf. also fig. 148 E). This primarily filamentous construction soon acquires the mature differentiation by the more or less considerable elongation of the internodal cell (figs. 147, 148 A). At the same time the nodal cell divides lengthwise into two (fig. 148 F, G, *1*), and this is followed by the successive appearance of a number of curved septa (*2*, *3*, *4*) cutting off a peripheral series (*p*) of usually six (sometimes eight, e.g. *Nitella opaca*, or ten[1]) cells from two central ones which latter subsequently undergo a few further longitudinal divisions (22, 23). The peripheral cells become protruded to form the apical cells of *laterals of limited growth* (fig. 148 E, *l*) which are cut off successively from the marginal segments of the node.

The laterals exhibit the same method of segmentation as the main axes, but the internodal cells commonly remain rather short (fig. 147 B) and sooner or later their apical cell ceases to divide, often assuming an elongate pointed shape. The successive whorls of these laterals of limited growth alternate, since the first longitudinal wall in the young nodal cell stands at an angle of about 30° to that in the next older node below, the shifting of the plane of division being in a counter-clockwise direction from below upwards ((7), (23) (1897) p. 164). The first-formed laterals of the whorls thus collectively lie on a spiral encircling the main axis, and this spiral arrangement is emphasised in older parts by a left-handed torsion of the internodes and of the cortical threads when these are present. Further whorled branching often takes place from the nodes of the primary laterals of limited growth, the oldest of these secondary branches always lying on the ventral side of the primary branch; these secondary branches do not generally alternate (fig. 147 A, B). By contrast to the long axes those of limited growth show a tendency towards torsion to the right (7).

The first segment cut off from the apical cell of a lateral becomes a nodal cell (fig. 148 E, *b*) which divides in the way described above to form the basal node (fig. 148 H, *b*). In *Nitella opaca* the lateral forms only one other node (18). It is from the basal node that *branches of unlimited growth* are produced and, as a general rule, these arise singly (fig. 147, *as*) from the oldest lateral of the whorl, although in some species of *Nitella* (*N. syncarpa*, fig. 148 D, *as*) a second branch develops from the next oldest lateral. These long branches are formed by the protrusion of a peripheral cell of the basal node of the short lateral on the side towards the apex of the main axis (fig. 148 H, *as*), so that such laterals of unlimited growth occupy a pseudo-axillary position (fig. 149 A, *as*). Their mode of origin recalls that of the long

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[1] When more than six peripheral cells are found in a node, these sometimes arise by a subsequent division of certain of the first-formed ones (22, 23).

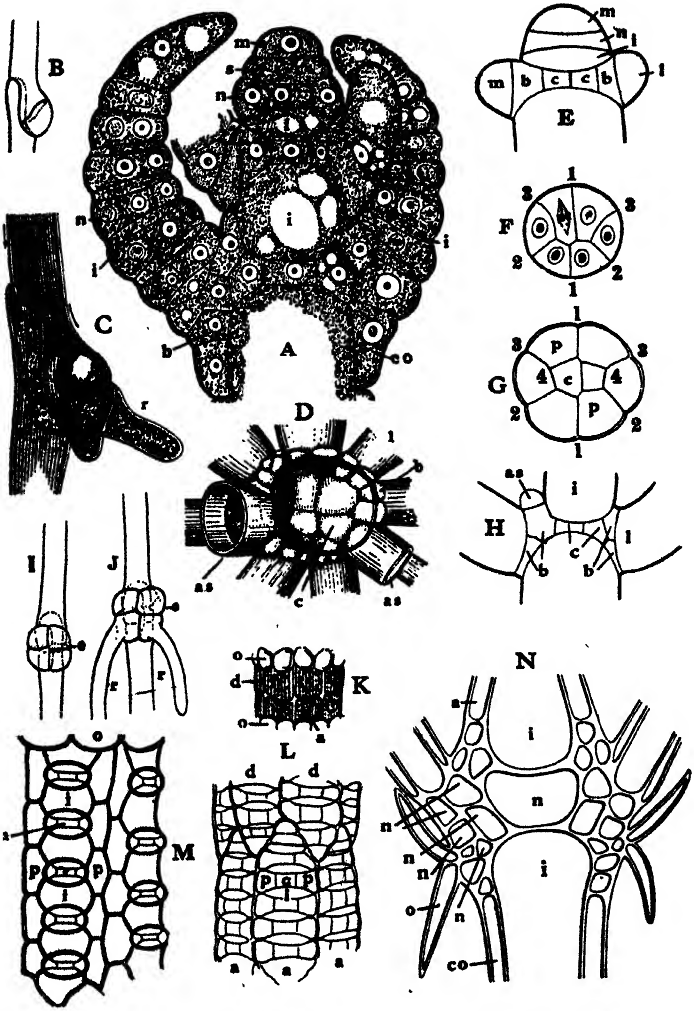

Fig. 148. Structure of Characeae. A, C, K–M, *Chara fragilis* Desv.; B, F, G, I, J, *C. aspera* (Deth.) Willd.; D, *Nitella syncarpa* (Thuill.) Kütz.; E, H, *N. gracilis* (Smith) Ag.; N, *Chara hispida* (L.) Wallr. A, apex of shoot

axes in the red alga *Batrachospermum* and other similar forms. The first segment cut off by the apical cell of the long lateral again divides to form a basal node.

If the main apical cell be damaged, growth is continued by the uppermost lateral of unlimited growth which, much as in a higher plant, gradually takes up a position in the continuity of the main axis; if all the long laterals are removed, a new growing point arises from a cell of the uppermost node (7, 63). The apical cell of a short lateral cannot be replaced and its destruction leads to a cessation of further development of the lateral.

The basal nodes of the short laterals are also the points of origin of the characteristic *cortication* found in most species of *Chara* and *Lychnothamnus* (29), but altogether lacking in *Nitella* and *Tolypella*. This cortication (cf. fig. 149 A) arises by the development from certain cells of each basal node of one upwardly (*a*) and one downwardly (*d*) growing thread. These threads remain closely apposed to the internodal cells and grow at the same rate as the latter so that the internodes are corticated from the very first (fig. 148 A, *co*); the upwardly growing thread from one node meets the downwardly growing one from the next node above (cf. the right-hand side of fig. 149 A). Where a long branch arises, however, the upwardly growing thread is suppressed.

The cortical threads show the same general morphological features as the other branches of the plant. Like them, they exhibit apical growth and undergo segmentation into nodes and internodes (fig. 148 L, M), the former dividing by two radial walls into a median (*c*) and two lateral (*p*) cells. In some species (e.g. *C. crinita* Wallr.) the latter remain small and the bulk of the cortication is due to the long internodal cells of the threads. In others (e.g. *C. fragilis* Desv.), however, the elongation of the internodes of the cortical threads, that accompanies the great growth in length of the underlying internode of the axis, is associated with a simultaneous elongation of the lateral cells of the nodes of the cortical threads (fig. 148 M). As a result three rows

showing method of segmentation; B, I, J, mode of branching of rhizoids; C, joint-formation in rhizoid; D, node seen from above; E, longitudinal section through apex; F, G, sections of young nodes showing the order of formation of the dividing walls; H, longitudinal section of a node; K, young internode with unicellular cortical threads; L, M, successively later stages in development of cortex; N, longitudinal section through node showing "stipules". *a*, ascending and *d*, descending cortical threads; *as*, axillary shoot; *b*, basal node of lateral; *c*, central cells of node; *co*, cortex; *e*, basal plate of rhizoid; *i*, internode; *l*, lateral of limited growth; *m*, apical cell; *n*, node; *o*, stipular outgrowths; *p*, peripheral cells of node; *r*, rhizoid; *s*, segment of apical cell. (A, K, L, M after Sachs; C after Pringsheim; N after Migula; the rest after Giesenhagen.)

of elongate cells correspond to each short lateral (cf. fig. 149 G), the middle row including the short median cells of the nodes of the cortical threads. In still other cases (e.g. *C. foetida* A. Br.) the elongating lateral cells of the nodes become interposed to form a single row of long cells separating the main series. In many species of *Chara* the short laterals develop a similar cortication.

The median cells of the nodes of the cortical threads divide by a tangential wall into a smaller inner and a larger outer cell (fig. 149 A, lower part, *pe*), which may merely form a slight protuberance but not uncommonly develops into a spine (cf. fig. 147 A) or may even divide into a number of cells, each furnishing a spine; such spines are morphologically comparable to laterals of limited growth. It will be clear from the preceding description that the development of the nodes of the cortical threads is a one-sided one, since the peripheral cells are cut off only on the outer and not on the inner side. Moreover, it will be realised that the cortical threads correspond to metamorphosed lateral branches of the basal node which are altogether suppressed in the genera lacking cortication.

In *Chara* (47) the basal nodes of the short laterals not uncommonly produce unicellular outgrowths, which are sometimes spinous, in one or more series underneath the lateral (fig. 148 N, *o*). In *Nitella hyalina* (20) these structures are branched. Such outgrowths have been called stipules, a term which is just as misleading in its implications as the designation leaves for the short laterals.

Attachment is effected by multicellular branched *rhizoids* (cf. fig. 152 *r*) with apical growth, arising from the peripheral cells of the lower nodes of the main axes, especially from those that are buried in the substratum. These rhizoids possess oblique septa (fig. 148 B) and do not show differentiation into nodes and internodes (cf. however (26)). The nucleus invariably lies at the apex of each cell, outside the domain of the rotating cytoplasm (cf. p. 453), and in the older cells assumes an elongate thread- or band-shaped form (44). At the septa the ends of the adjacent cells are protruded in opposite directions (fig. 148 B, C) so as to form a kind of joint, whilst from the protrusion of the upper cell a segment is cut off which, dividing into quadrants followed usually by further septa, gives rise to tufts of branch-rhizoids (fig. 148 C, I, J); these may branch further in the same manner. The plate of cells (*e*) from which these rhizoids originate can be interpreted as a basal node.

Every node probably possesses a potential capacity to form rhizoids, their normal production only at the lower (older) nodes being due to an inhibiting influence of the apical cell, since if the latter be removed, rhizoids also develop from the younger nodes (7, 63). The rhizoids function as organs of attachment, but also play a considerable part in the absorption of mineral salts (80, 81).

CELL-STRUCTURE

The cells of the Characeae contain numerous small discoid chloroplasts, of oval shape and devoid of pyrenoids, lodged in the peripheral layer of the parietal cytoplasm. Except in the elongated internodal cells the protoplasmic contents are dense; the single nucleus is usually centrally placed and in older cells contains a considerable number of nucleoli (fig. 148 A). All the greatly enlarged cells have a huge central vacuole, and in these the nucleus becomes lobed and gradually multiplies by a process of amitosis (34, 68, 74). The resulting nuclei are distinguished by the possession of large nucleoli and scanty chromatin.

The mitotic division of the nucleus has been studied by diverse investigators and shows essentially the same features as in higher plants.[1] There is difference of opinion as to the occurrence of centrosomes which would, however, appear to be lacking. The nuclei of the nodes are from the beginning much larger than those of the internodal cells (15, 74). The number of chromosomes varies greatly in the different species (43). The cells usually contain, apart from the nuclei, deeply staining masses which various investigators believe to be extruded from the nucleoli (48, 64), although this is denied by Karling (37).

In the elongate cells the chloroplasts are arranged in well-marked longitudinal series which show a spiral trend in the internodes of the long axes, although this is not recognisable or little marked in the laterals of limited growth. The less dense part of the parietal cytoplasm, internal to that containing the chloroplasts, is in a state of constant rotation in the longitudinal direction, and within each internodal cell there is an upward stream on the one and a downward stream on the other side (cf. (8), (42), (45), (53)). The line of separation is marked on either flank of the cell by a colourless streak, where the dense arrangement of the chloroplasts in the lining cytoplasm is interrupted and where, according to Votava (79), the membrane possesses an inwardly projecting ridge that serves to segregate the two streams.

The orientation of the streams in the internodes of the long axes is related to the position of the whorl of short laterals above, the ascending stream being situated below the oldest, the descending one below the youngest member of the whorl. As a consequence the colourless streak that marks the line of separation of the two streams is oblique and follows a steep spiral course around the axis. In the laterals of limited growth the ascending stream is on the abaxial and the descending on the adaxial side. In the cells of the nodes the rotation of the cytoplasm is in the transverse sense. The development of laterals of unlimited growth is favoured on the side corresponding to the ascending stream,

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[1] See (15), (16), (35), (37), (43), (55), (58*a*), (70), (73), (83).

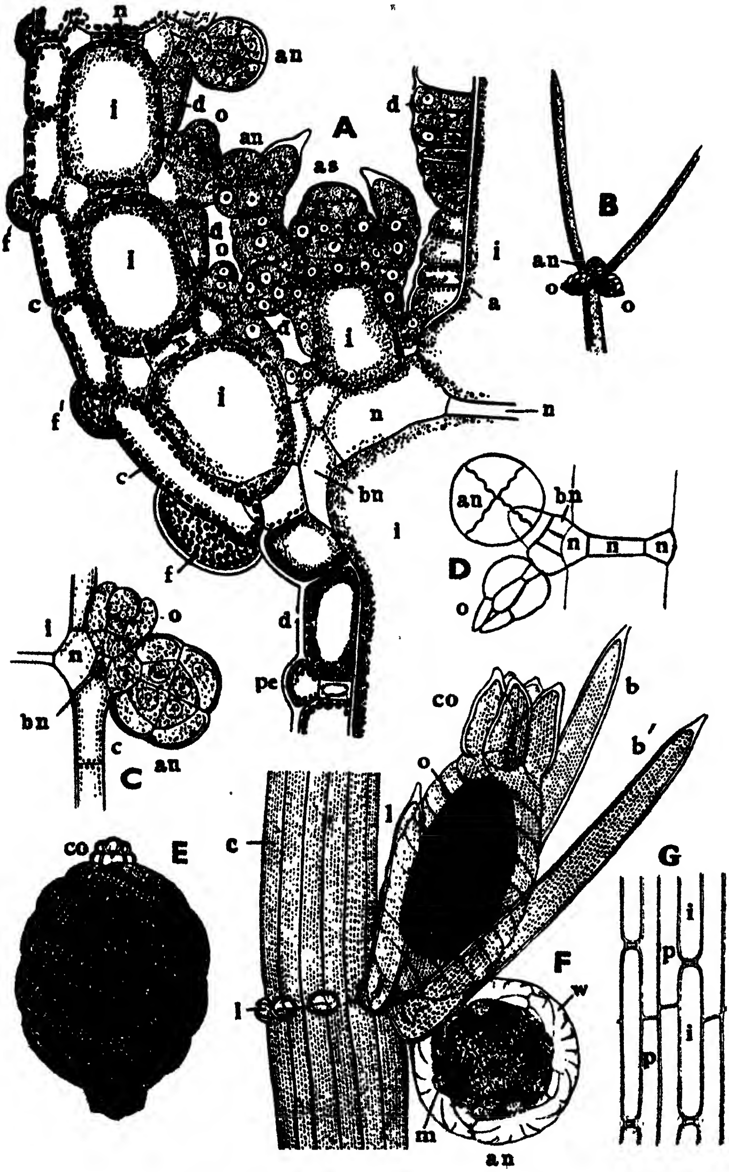

Fig. 149 [*for description see opposite*]

that of rhizoids on the side corresponding to the descending stream in the underlying internode (8). According to Cazalas (11) young cells do not exhibit rotation of the cytoplasm.

The membrane (14, 85), apart from a superficial layer of unknown composition, consists of cellulose. The superficial layer is more or less gelatinous and appears to be the seat of deposition of the carbonate of lime. The cellulose layer is commonly provided with irregular internal thickenings. Of the diverse cell-inclusions that have been noted it is only necessary to mention curious protein-bodies—in some species provided with numerous fine spinous protrusions—found especially in the internodal cells (57, 79) and highly refractive granules occurring in the rhizoids and interpreted by some (24, 71) as statoliths (cf. however (86)).

SEXUAL REPRODUCTION

In their oogamous reproduction the Charales betray their marked specialisation no less than in the elaborate vegetative organisation. The large spherical, bright yellow or red antheridia and the oval oogonia with their envelope of spirally arranged bright green threads (figs. 147 C, 149 B) are conspicuous objects, visible to the naked eye when mature. As Karling (36) and others (26, 80) have shown, light is the most important factor in their development. As a general rule oogonia and antheridia occur in close juxtaposition, but a considerable number of dioecious forms are known and the monoecious ones often show marked protandry (fig. 150 N). Both kinds of sex organs are usually borne on secondary laterals of limited growth, originating from the upper nodes of the primary laterals, although in *Tolypella* they may also arise from the basal nodes of the latter.

The antheridia generally take the place of the oldest secondary branch of the node, so that they occupy a ventral position on the primary lateral (fig. 149 C, F, *an*). As a general rule the lateral in question produces a basal node (fig. 150 N, *bn*) and then its apical cell divides in the manner described below to form an antheridium;

Fig. 149. A, C, F, G, *Chara fragilis* Desv.; A, structure of a node with an axillary shoot (*as*) and young sex organs; C, developing sex organs; F, mature antheridium and oogonium; G, small part of cortex enlarged. B, E, *Nitella flexilis* Ag.; B, antheridium and two oogonia; E, almost mature fruit. D, *Lamprothamnium papulosum* (Wallr.) Groves, structure of a fertile node. *a*, ascending cortical thread; *an*, antheridium; *b*, *b′*, branchlets of basal node of antheridium ("bracteoles"); *bn*, basal node of lateral; *c*, cortex; *co*, corona; *d*, descending cortical thread; *f*, *f′*, stipular outgrowths; *i*, internode; *l*, lateral; *m*, manubrium; *n*, node; *o*, oogonium; *p*, peripheral cell of node of cortex; *pe*, external cell of node of cortex; *w*, wall of antheridium. (D after Braun; G after Printz; the rest after Sachs.)

the latter thus usually represents a metamorphosed secondary lateral. In some species of *Nitella*, however, the antheridia may replace a primary lateral. The basal node of the antheridium, in forms possessing cortication, gives rise in the usual way to a cortical thread on its lower side, but in all monoecious species a cell on the adaxial side produces the oogonium which thus represents a branch of a higher order (figs. 149 C, 150 N, *o*). The sex organs are therefore generally so placed that the oogonium is directed upwards and the antheridium downwards (fig. 149 F); even in dioecious species the same orientation is recognisable. In *Lamprothamnium*, however, the oogonium arises from the abaxial side of the basal node of the antheridium (fig. 149 D) so that the position of the two organs is reversed. From the flanks of the basal node of the antheridium elongate one-celled branchlets ("bracteoles") arise, one on either side (fig. 149 F, *b*, *b'*), which together with a few similar branches (*l*) formed from the node of the primary lateral constitute a loose envelope about the oogonium. In the female plant of dioecious species the place of the antheridium is taken by an ordinary lateral ("bract") from whose basal node the oogonium arises.

The apical cell of the lateral destined to form an antheridium[1] (65, 76) cuts off one or two discoid cells (fig. 150 A, B, *s*) at its base and then assumes a spherical shape. Thereupon, it undergoes division into octants by two longitudinal walls, followed by a transverse one (fig. 150 A, B). In each octant there then arise two successive periclinal walls so that eight diagonal series of three cells each are produced (fig. 150 B, C), of which only the innermost one undergoes any further division. Very considerable enlargement, however, takes place in the course of further development, so that the inner segments gradually become separated from one another. The eight peripheral cells (fig. 150 C, N, *w*) develop into curved plates (*shields*) with the convex surface outwards and with a characteristic infolding of their membranes (fig. 149 F, *w*) making the wall of the antheridium appear many-celled in longitudinal sections (fig. 150 N, *w*); as the male organ matures, the shields acquire red-coloured contents. The antheridial wall is completed at the base by one of the discoid cells first cut off which usually protrudes markedly into the cavity of the antheridium (fig. 150 N, *s'*). The middle segment of each primary diagonal series undergoes considerable radial elongation, forming the rod-shaped *manubrium* (figs. 149 F; 150 D, *m*) which arises from the centre of the shield and bears at its inner end one or more rounded cells, the *capitula*, derived from the innermost of the primary segments (fig. 150 D, N, *c*).

The cells of the capitulum (fig. 150 D) give rise on their inner side

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[1] Diverse deviations from the normal structure of the antheridia are described by Karling (38).

to about six *secondary capitula* (*sc*), from each of which there develop long threads (*t*), usually twice forked at their base (fig. 150 D); as the antheridium enlarges, these threads gradually fill the cavity with a dense tangle. Each of these *spermatogenous threads* ultimately consists

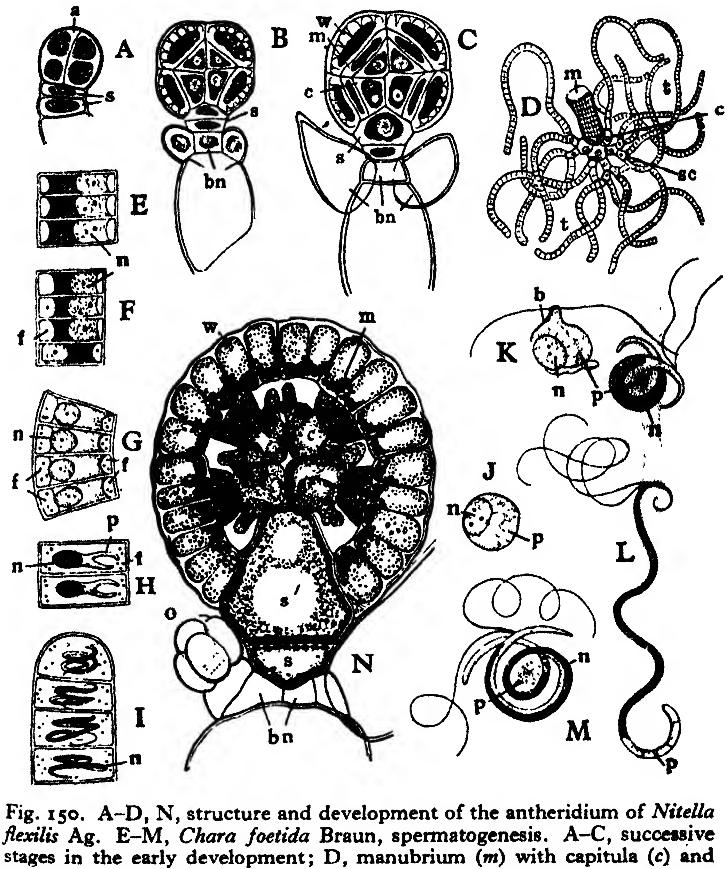

Fig. 150. A–D, N, structure and development of the antheridium of *Nitella flexilis* Ag. E–M, *Chara foetida* Braun, spermatogenesis. A–C, successive stages in the early development; D, manubrium (*m*) with capitula (*c*) and spermatogenous threads (*t*); E–I, sequence of changes in spermatogenous cells during the early development of the spermatozoids; J, K, M, successive changes in the protoplast of same (membrane omitted); L, mature spermatozoid; N, young antheridium. *a*, antheridium; *b*, blepharoplast; *bn*, basal node of antheridium; *c*, capitulum; *f*, flagella; *m*, manubrium; *n*, nucleus of spermatogenous cell; *o*, young oogonium; *p*, protoplasm of spermatogenous cell; *s*, *s'*, basal cells of antheridium; *sc*, secondary capitulum; *t*, spermatogenous threads; *w*, wall of antheridium. (E–M after Belajeff; the rest after Sachs.)

of one or two hundred discoid spermatozoid mother-cells. In the development of the threads cell-division takes place more or less simultaneously in groups of cells (39, 75), and before spermatogenesis sets in the nucleoli disappear (83).

In the formation of the spermatozoids the large nucleus of the mother-cell shifts to one side, while the protoplast develops a shallow transverse furrow (fig. 150 E, F). A prominent blepharoplast appears in the neighbourhood of the nucleus (fig. 150 K, *b*) and, as the two long flagella arise from it, they extend into the furrow surrounding the protoplast and gradually encircle the latter several times (cf. fig. 150 F, G, *f*). Meanwhile the protoplast develops two outgrowths (fig. 150 H, K, *p*), one at the apical and the other at the opposite end of the cell, which lengthen to form the protoplasmic body at the two extremities of the future spermatozoid. At the same time the nucleus, which now appears altogether homogeneous, elongates to form a spiral band-shaped structure (fig. 150 I, K, *n*), the small amount of remaining cytoplasm of the mother-cell giving rise to a delicate layer situated mainly on the inner side of the nuclear loops (fig. 150 M). The male cells are liberated by the falling apart of the shields of the antheridial wall and the subsequent gelatinisation of the walls of the mother-cells. The liberated sperm (fig. 150 L) appears prominently elongated, the accompanying cytoplasm being clearly marked at the anterior and posterior extremities, while the two long flagella arise a little way behind the front end, although Mühldorf (51) states that they arise apically.

The development of the spermatozoids of Characeae has been investigated by many botanists,[1] and the only essential point of disagreement lies in the origin of the blepharoplast which is bound up with the usual difference of opinion as to its nature. According to some it is a centrosome, according to others a structure *sui generis*. Belajeff ((4); cf. also (46 *a*)) found that the anterior part of the body bearing the flagella had an origin distinct from the posterior part, the former arising at the boundary between cytoplasm and nucleus as a small cytoplasmic protuberance which elongated subsequent to the development of the flagella, so that the latter at first terminal, later assumed the lateral position. He distinguished a delicate deeply staining thread extending between the nucleus and this protuberance. According to Mottier (50), however, the whole cytoplasmic body arises as a delicate thread-like differentiation of the plasma-membrane, extending partly round the cell and embracing the nucleus in its arc; it is elongate from the first. The general features of the development of the spermatozoids of Characeae do not differ in any appreciable respects from that of archegoniate plants.

Hofmeister (32) already suggested that the antheridia of Characeae

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[1] See (4), (43), (46 *a*), (50), (83).

should be regarded as compound structures, actually comprising a large number of male organs (cf. also (66)). This view has recently been elaborated by Goebel (27), who regards the eight primary octants as representing secondary laterals of the antheridial axis which divide into three cells differentiating into shield, manubrium, and capitulum. The manubria occupy the position of internodal cells, whilst the overlying cells remain congenitally fused. The capitulum corresponds to the basal node of the secondary lateral and bears the spermatogenous threads, much as the basal nodes in the vegetative parts may bear cortical threads. On this very ingenious interpretation the actual antheridia are single-celled structures, like those of most other Algae. It must be noted, however, that in the development of the spermatozoids and in the character of the latter the antheridia of Characeae diverge rather considerably from those of other Algae.

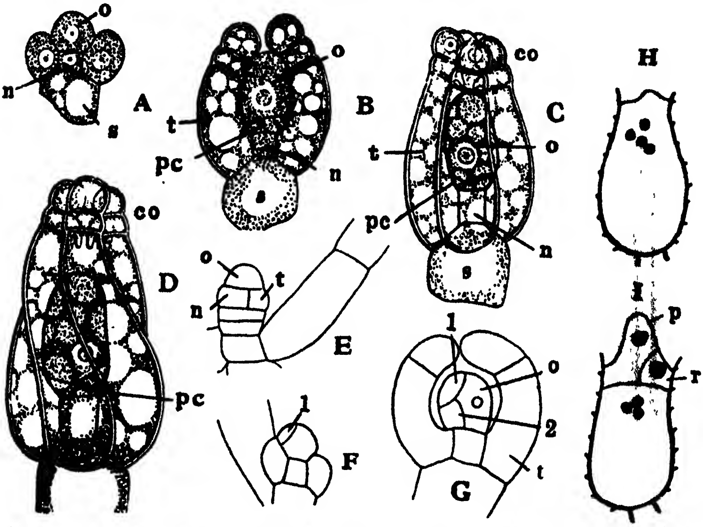

Fig. 151. Development of the oogonium. A–D, *Nitella flexilis* Ag. (after Sachs), four successive stages. E–G, *N. subtilissima* Br. (after Goebel), first divisions in young oogonium. H, I, *Chara foetida* A. Br. (after Oehlkers); H, after reduction, with four nuclei; I, two-celled proembryo formed from the successful nucleus. *co*, corona; *n*, node of oogonium; *o*, oogonium; *p*, protonemal cell; *pc*, cells cut off at base of oogonium; *r*, rhizoid; *s*, stalk-cell; *t*, enveloping threads.

The cell of the basal node of the antheridium that develops into an oogonium (cf. p. 456) undergoes two transverse divisions (fig. 151 A) to form a row of three cells (16, 25, 28, 65). Of these the uppermost gives rise to the oogonium (*o*) by great enlargement, the lowest forms the one-celled stalk (*s*) which is outwardly often scarcely recognisable, while the middle cell constitutes a node (*n*) which divides into a central and five peripheral cells. The latter grow out into the five threads that invest the oogonium already in early stages (fig. 151 B, *t*), and that soon cut off one (*Chara*, fig. 149 F, *co*; *Lamprothamnium*) or two (*Nitella*, fig. 151 C, D, *co*; *Tolypella*) small coronal cells at their apices. In the course of the further development the enveloping threads, without undergoing septation, elongate very considerably, thicken their walls, and gradually assume the spiral course (always clockwise) that characterises the mature condition (fig. 149 E, F). The coronal cells, however, remain small and erect.

The single ovum within the oogonium accumulates vast quantities of starch as well as oil (49), but the apex remains clear and is occupied by finely granular cytoplasm constituting the receptive spot; the nucleus is basal in position. At an early stage one or more cells are cut off at the base of the young oogonium, a single one in *Chara*, three successive ones in *Nitella* (fig. 151 B–D, *pc*). In the latter the first two cells are cut off by walls that run more or less longitudinally (fig. 151 F, G, *1*, *2*), while the third division-wall is definitely transverse. Goebel (25) concluded from this sequence of division in *Nitella* that the three septa are to be homologised with those that arise in the young antheridia and lead to the formation of octants, so that in the case of the oogonium only a single octant would be fertile. Goetz (28), on the other hand, regarded these cells as perhaps representing the remnants of a former multicellular wall around the ovum. In connection with Goebel's hypothesis mention may be made of those cases in which spermatogenous threads have been found within malformed oogonia.[1]

Beneath the corona, whose cells fit closely together, the enveloping threads become dilated, so that the space between the corona and the apex of the oogonium, which is occupied by a mucilaginous liquid, becomes markedly narrowed down in its middle, assuming the shape of an hour-glass. Shortly before fertilisation (2) the portions of the threads surrounding the upper part of this space lengthen to form a kind of neck and then separate slightly from one another so that narrow slits arise through which the spermatozoids penetrate. In other cases the enveloping threads break down just below the corona. At the time of fertilisation the apex of the oogonial wall gelatinises. The spermatozoid nucleus has to traverse the whole of the ovum to fuse with the nucleus of the latter.

Parthenogenesis is known in *Chara crinita* (21, 74, 84), a species which in southern latitudes in part produces normal male and female plants with twelve chromosomes, the ova of such plants being capable of

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[1] There is an extensive literature dealing with malformations of this and other kinds (cf. (19), (26), (46), (69), (82)).

further development only if they are fertilised. In the same localities, however, Ernst (21) found a slightly different form bearing oogonia only and possessed of twenty-four chromosomes; in more northern latitudes this form alone occurs. The ova of this diploid type always develop parthenogenetically. Ernst is of the opinion that it represents a hybrid between *Chara crinita* and a second unknown parent, the characters of the female parent preponderating. This point of view has been criticised by Winkler ((84) p. 3). Artificial parthenogenesis has been induced in a number of dioecious species of *Chara* (21).

EMBRYOLOGY (3, 52, 54, 60, 61)

After fertilisation the zygote nucleus wanders to the apex of the ovum, while the latter secretes a cellulose membrane which later takes on a yellow or brown coloration. External to this lies the oogonial wall, and beyond that the enveloping threads whose inner membranes undergo thickening and gradually assume a dark colour; they are stated to become suberised (57) and may also be silicified. The remaining walls do not thicken. The hard envelope that is thus created often shows diverse sculpturings. There is usually (except in *Nitella*) an external covering of lime, which is deposited in the cell-cavities of the enveloping threads and is developed to a very varying extent. The chloroplasts in the threads take on a yellow or red coloration.

At the commencement of germination the colourless cytoplasm at the apex of the oospore increases in amount and two successive nuclear divisions (fig. 151 H) take place. Oehlkers (55) produces evidence that the first of these is the reduction division so that, as in other oogamous Green Algae, the zygote is the only diploid phase in the life-cycle. Tuttle's (77) statement as to the occurrence of reduction during gametogenesis has not been confirmed (cf. also (15), (16), (43)). The formation of the four nuclei is followed by the appearance of a septum across the apex of the oospore, whereby the latter is divided into two very unequal parts, the upper cell harbouring one of the haploid nuclei, while the remaining three are found in the lower part which is richly stocked with food-reserves (fig. 151 I). These three nuclei subsequently disintegrate. The enveloping membranes break open apically (fig. 152 A) and thereupon the upper cell divides longitudinally (fig. 151 I). The two daughter-cells (fig. 152 A, *p*, *r*) resulting from the division grow out in opposite directions to form the first rhizoid and a lengthening erect thread, the *protonema*, which becomes green and undergoes a number of transverse divisions (fig. 152 B, *p*). Soon further events centre in the second cell from the base of this protonema which has been carried aloft by the elongation of the rather pale-coloured basal cell (fig. 152 B, *1*).

The cell in question (fig. 152 B, *2*) divides transversely into three, the upper and lower segments (*sn*, *rn*) developing into nodes which become gradually separated by the very considerable elongation of the intervening internodal segment (*i*) (cf. also fig. 152 D). In both nodes longitudinal divisions lead to the formation of a transverse plate of cells, those in the upper (*sn*) taking place according to the usual method of nodal segmentation, while in the lower node (*rn*)

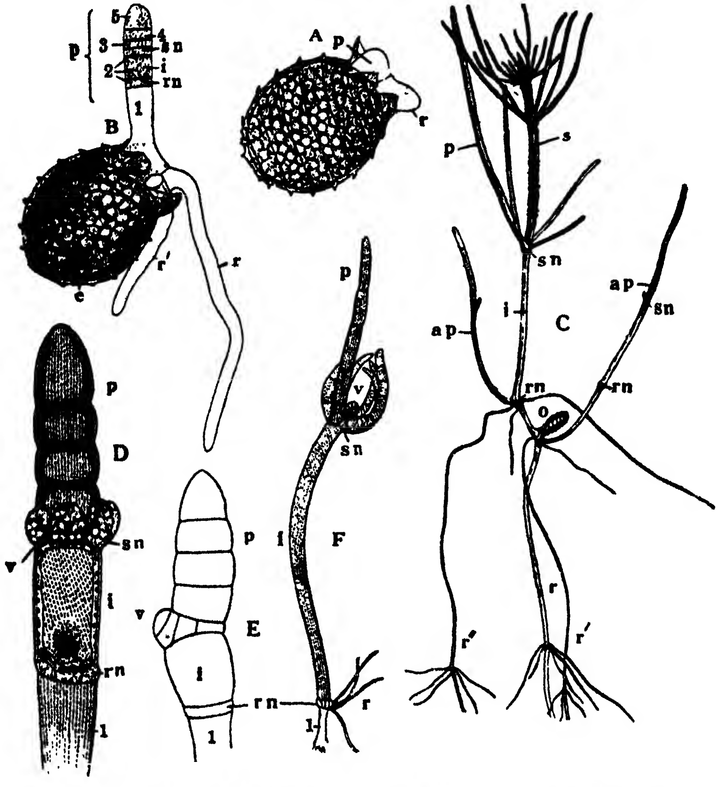

Fig. 152. The early development of Characeae; A, B, *Tolypella glomerata* (Desv.) Lamk.; C, *Chara crinita* Wallr.; D–F, *C. fragilis* Desv. A, B, rupture of oospore-membranes and development of young protonema, etc.; C, older proembryo with developing shoot of mature plant (*s*) and accessory protonemal threads (*ap*) arising from the rhizoid-node and from the base of the protonema; D, upper part of protonema showing laterals arising at the shoot-node; E, still younger stage, showing divisions leading to formation of mature shoot; F, protonema intermediate between B and C, with the future plant (*v*) developing at the shoot-node. *ap*, accessory protonema; *e*, envelope of oospore; *i*, internode; *o*, oospore; *p*, protonema; *r*, *r'*, *r''* rhizoids; *rn*, rhizoid-node; *s*, mature plant; *sn*, stem-node; *v*, early stage of mature shoot. (D–F after Pringsheim; the rest after De Bary.)

the divisions are somewhat more irregular. The peripheral cells of the latter grow out into rhizoids (fig. 152 C, *r''*; F, *r*), which supplement the primary rhizoid. The peripheral cells of the upper node give rise to a whorl of short, little developed laterals (fig. 152 D, F, *sn*), with the exception of the oldest peripheral segment from which is developed the future plant (fig. 152 D, F, *v*). As the axis of the latter (fig. 152 C, *s*) elongates, it assumes an erect position and the apical part of the original protonemal thread (*p*) is turned to one side. Where the primary rhizoid (*r*) emerges from the oospore (*o*), a sometimes several-layered basal node is formed from which additional rhizoids (*r'*) are produced. It may be well to emphasise two facts with respect to the embryology of the Characeae, viz. that the protonema is formed only from a small part of the oospore and that the mature plant arises as a lateral branch from the protonema (cf. especially fig. 152 F).

VEGETATIVE REPRODUCTION

Vegetative propagation may occur at all stages in the life of the Characeous plant. Secondary protonemata, that may even develop more rapidly than the primary one, often originate from the rhizoidal node of the protonema, as well as from the basal node of the primary rhizoid (fig. 152 C, *ap*). Similarly, secondary protonemata have been found to develop from certain cells (dormant apices) of the surviving nodes of older plants after hibernation (60, 61) or from those of fragments including nodes placed under suitable cultural conditions (61, 63). The further development of such protonemata always follows the lines described above.[1]

Oltmanns ((56) p. 445) regards certain peculiarly developed branches that arise from the nodes of hibernating *Chara*-plants in the spring as being of an analogous nature. These long branches develop not only from the basal nodes of the laterals in the usual way, but may originate from any one of the nodal cells, and they are distinguished by the fact that the lower internodes are naked ("nacktfüssige Zweige" of Pringsheim (61)), or have an imperfectly developed cortication (fig. 153 E). Sometimes the cortical threads of such laterals are not apposed to the internodes but stand off like ordinary branches, such cases rendering their morphological nature particularly clear. Naked branches of this kind and secondary protonemata may occur at the same node. In *Nitella opaca* protonemata and other adventitious branches can arise also from the upper node of the lateral. It appears that all such developments do not occur in the intact plant, where the growing apices exert an inhibiting effect (18).

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[1] Drew (17), however, describes a case in which such a protonema showed a tendency to continue apical growth.

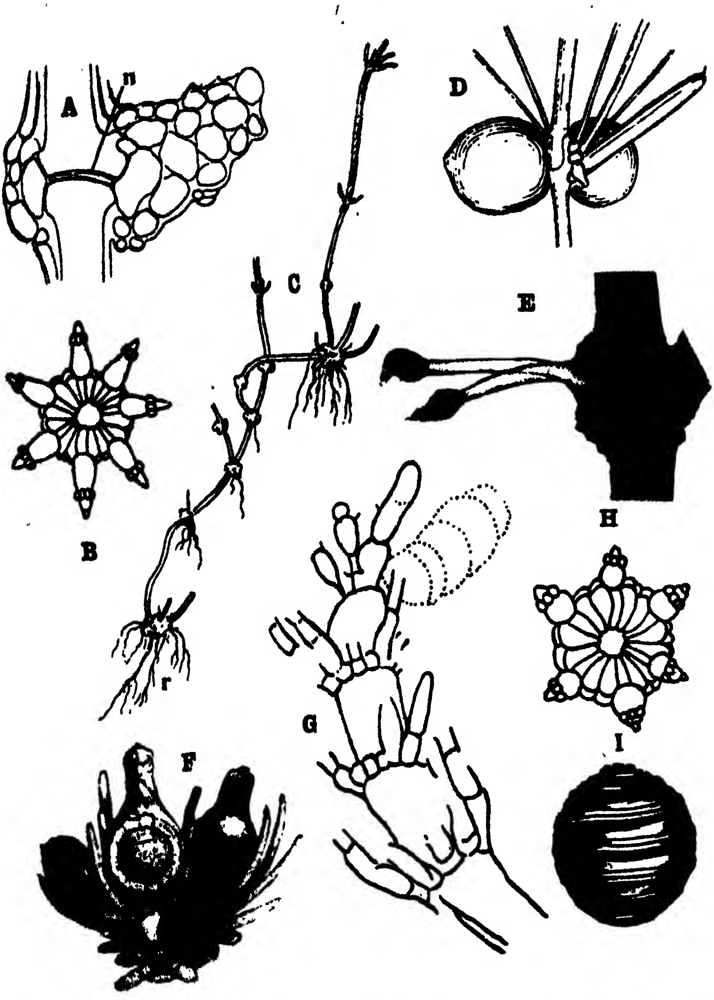

Fig. 153. A, C, *Chara baltica* Bruzelius; A, section of one of the tuber-like growths shown in C. B, H, *Nitellopsis obtusa* J. Groves, starch-stars. D, *Chara aspera* (Deth.) Willd., underground bulbils. E, *C. fragilis* Desv., naked branches. F, *Lagynophora liburnica* Stache. G, *Algites* (*Palaeonitella*) *Cranii* Kidst. & Lang (Middle Devonian). I, *Gyrogonites medicaginula* Lmk. (Eocene). *n*, node; *r*, rhizoid. (B, H after Groves & Bullock-Webster; E after Pringsheim; F after Stache; G after Kidston & Lang; I after Schimper and Schenck; the rest after Giesenhagen.)

Many Characeae produce special organs of vegetative propagation (22, 41, 47, 52). Tuber-like growths are commonly formed on the rhizoids or around the nodes of the buried parts of the main axes. Those of the rhizoids in some cases appear as great enlargements of some of the four cells (cf. fig. 148 I, J) from which branch-rhizoids normally originate (fig. 153 D); these cells become filled with starch and cut off a basal node, as well as a number of cells at their apex. In other cases, however, the four cells divide irregularly to form a multicellular mass, and such irregular tuberous growths are also often produced by proliferation of the peripheral cells of the nodes of the buried axes (fig. 153 A, C). The so-called starch-stars (fig. 153 B, H), met with in various members of the family, are likewise nothing else than subterranean nodes in which the laterals have developed to a certain extent and all the cells are copiously filled with starch.

THE POSITION OF THE CHARALES AMONG THE ALGAE

The envelope of lime deposited around the oospore is formed only within the spiral threads, not in the stalk-cell, nor in the corona. If the organic parts decay, there thus remains a hollow calcareous body with a basal aperture, often showing clearly the spiral arrangement of the envelope. It is in the condition of such fossilised fruits (fig. 153 I) that most Characeous remains are found ((30), (59) p. 88). Since the corona is lacking an assignation to the Nitelleae or Chareae is impossible. In the vast majority of cases such fossil fruits have five enveloping threads as in the recent forms, but in the Carboniferous *Palaeochara* (5) there are six. All the others are referred by Pia (59) to Lamarck's genus *Gyrogonites* (fig. 153 I), found from the Lias onwards.

Another form, *Lagynophora*, only known from the Palaeozoic, has lageniform fruits which are axillary to the short laterals (fig. 153 F); they appear to have belonged to a form with cortication. A considerable number of other fruit-bodies, that have been assigned to the Characeae, diverge rather more markedly from the normal, and the evidence for their inclusion in this family is at present quite inadequate. Various vegetative remains have been regarded as belonging to members of this family, for instance Kidston's and Lang's *Palaeonitella* (40) (fig. 153 G), but whilst there is some measure of probability a certain assignation is impossible in the absence of cell-contents. Pia (59 a) regards the genus *Piaea* (cf. p. 401) as hinting at a possible common origin for Dasycladaceae and Charales.

The fossil evidence does not help in elucidating the origin and affinities of the Charales. Their position can therefore only be determined by reference to the recent forms. As already mentioned at the outset most authorities have regarded them as representing a special class, the Charophyta, and it is undoubtedly possible to bring forward good reasons for this attitude. At the same time the differences between the Charales and the main body of the Chlorophyceae are scarcely quite of the nature of those that serve to separate other classes of the Algae. True, there is a marked advance in vegetative organisation and a great elaboration of the sexual reproductive organs, but the former feature does not afford any sharper contrast than can be found, for instance, among Ectocarpales between the simple and more specialised forms. Indications for practically all the tendencies that characterise the Charales are to be found in other orders of Chlorophyceae and, were the fossil record relating to the latter more perfect, it is to be suspected that all transitions to the complexities of the Characeae would be found. If Goebel's interpretation of the antheridium (cf. p. 459) be accepted, one of the most outstanding characteristics acquires a rather simpler explanation. The Characeae have been regarded as a remnant of the many probable evolutionary lines that attempted to colonise the land (12), but it is clear that they diverge very widely from the normal character of the higher plant.

The occurrence of green chloroplasts and starch, the haploid character, and the relatively simple vegetative organisation of the Nitelleae, all speak for the Charales as representing merely a very highly specialised side-line of the Chlorophyceae.

The members of the single family, Characeae, are usually grouped as follows:

(*a*) *Nitelleae:* Nitella, Tolypella.
(*b*) *Chareae:* Chara, Lamprothamnium, Lychnothamnus, Nitellopsis.

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Class II. XANTHOPHYCEAE (HETEROKONTAE)[1]

This class was first clearly distinguished by Luther (53) in 1899, who gave it the name Heterokontae. The close relationship between certain of the Algae included in it had been recognised much earlier by Borzi ((10) p. 199), but it was the discovery of definite flagellate representatives (Heterochloridales) that paved the way to a proper comprehension of its distinctive features. As a matter of fact there are few other classes in which a motile ancestry is as clearly patent as in this case, and it has contributed more than any other to the firm establishment of the doctrine of flagellate evolution of the Algae. When first segregated from the Chlorophyceae this class of the Yellow-Green Algae included only relatively few forms, but during the present century many additional members have been discovered, and it has become increasingly apparent that there exists a far-going parallelism between the two classes, to which Pascher (60) first drew attention. Nevertheless the total number of genera and species is small, the Xanthophyceae apparently not exhibiting anything approaching the multiplicity of form to be seen among the Chlorophyceae.

The general characteristics of the class have been summarised on p. 5 and need not be repeated here. The classification, in view of the above-mentioned parallelism, follows essentially the same lines as in the Chlorophyceae, the following orders being distinguished:

(I) Heterochloridales, including the motile forms and their immediate derivatives.

(II) Heterococcales, including the coccoid forms.

(III) Heterotrichales, including the filamentous forms.

(IV) Heterosiphonales, including the siphoneous forms.

Order I. *HETEROCHLORIDALES*

(*a*) THE MOTILE UNICELLULAR FORMS (HETEROCHLORINEAE)

The motile members of this class are naked unicells and but relatively few are known; motile colonial types have not so far been found. The first form that was described, *Chloramoeba* (6), introduces us at once to the principal characteristics of the class. The original species has

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[1] The name Xanthophyceae, proposed by Allorge (1), although open to certain objections (cf. (32)), has the great advantage of affording a designation uniform with that of other classes of the Algae and has therefore been adopted here in preference to the usual name Heterokontae.

so far only been observed in cultures containing brackish water, but a second (*C. marina* Schiller (88) p. 76) has been found in coastal waters in the Adriatic, while Doflein (24) has described a freshwater form showing holozoic nutrition. The living individuals have a very variable outline owing to the soft nature of the periplast (fig. 154 A). The front end is broad and more or less truncated and bears two very unequal flagella which are inserted in close proximity. One flagellum is about twice the length of the cell, whilst the other is a very short curved structure. This inequality of the flagella is characteristic of nearly all Xanthophyceae. The longer flagellum, after special staining, shows numerous fine lashes ((99), and fig. 154 H, K). According to Doflein (24) the flagella in *Chloramoeba* are attached to a common rhizoplast connected with the nucleus. Beneath their point of origin lies a contractile vacuole (fig. 154 A, *v*).

The cells contain a single nucleus and 2–6 discoid chloroplasts which, as in all Xanthophyceae, show a yellow-green colour owing to the presence of an excess of xanthophyll.[1] This characteristic of the plastids is invariably associated with an absence of starch, drops of oil occurring as the usual reserve-food. These facts are no doubt indicative of a metabolism essentially different from that of the Chlorophyceae. The cells of *Chloramoeba* also contain glycogen ((81) p. 380). Schiller (88) and Doflein (24) record pyrenoid-like bodies[2] in the chloroplasts. For the rest the protoplast has a remarkably clear appearance, being practically devoid of granular inclusions, a feature which is met with rather commonly in the class ((69) p. 227). If supplied with organic nutriment, *Chloramoeba* can thrive for prolonged periods in darkness and at such times loses its plastids and becomes colourless[3] (cf. *Euglena*, p. 735).

A further interesting form is *Heterochloris* ((66) p. 23), probably an inhabitant of brackish water. In its flagellate stage (fig. 154 B) it appears pear-shaped and shows a faint emargination of the periplast on one side so that the cells are slightly dorsiventral. The individuals are, however, strongly metabolic (fig. 154 C) and may at times assume a completely rhizopodial form, with or without loss of the two flagella (fig. 154 D). There are only two relatively small chloroplasts which lie at the sides of the cell in the plane of the flagella. Apart from oil,

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[1] This is shown by the blue coloration obtained on heating with strong hydrochloric acid, a useful means for recognising doubtful members of the class. Poulton ((80) p. 25) describes a method by means of which the relative amounts of xanthophyll in members of Xanthophyceae and Chlorophyceae can be demonstrated by crystallisation within the cells.

[2] Similar bodies have also been observed in *Bumilleria*, *Tribonema*, *Botrydium* (pp. 493, 497), and others.

[3] Doflein (24) suggests that *Chloramoeba* may be a colourless form with symbiotic green cells (cf. also (66) p. 22), since the organisation of the protoplast is much like that of a member of Rhizomastigaceae.

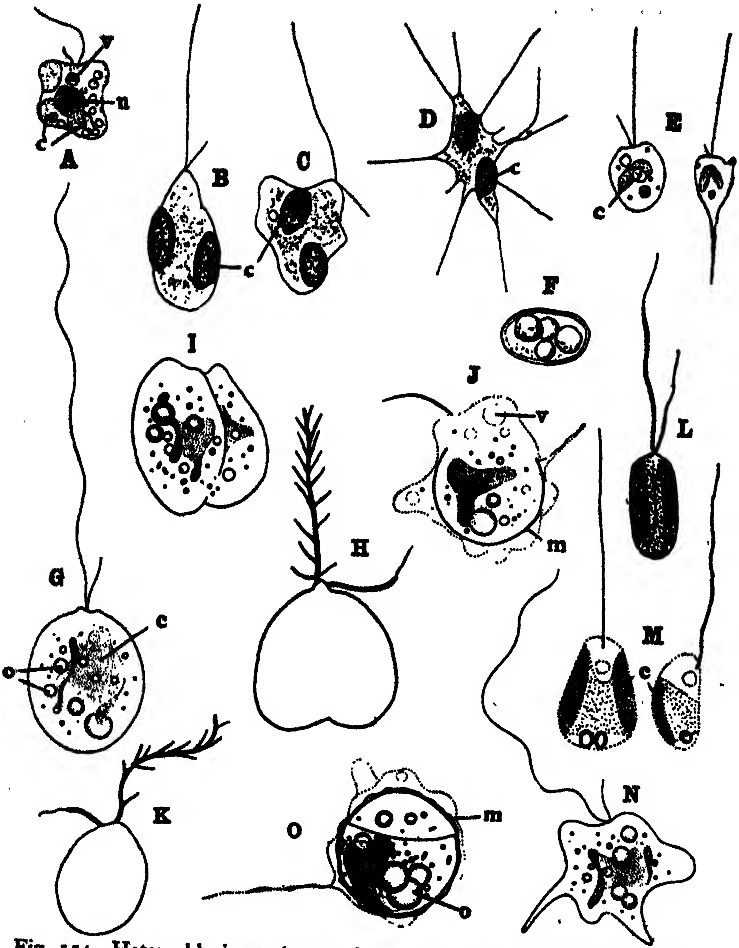

Fig. 154. Heterochlorineae (except H and K). A, F, *Chloramoeba heteromorpha* Bohlin (after Bohlin); F, cyst. B–D, *Heterochloris mutabilis* Pascher (after Pascher); B, flagellate, C, amoeboid and D, rhizopodial stages. E, *Chlorochromonas minuta* Lewis (after Lewis), on the left a contracted, on the right a drawn out individual. G, I, J, N, O, *Chloromeson agile* Pascher (after Pascher); G, normal and N, amoeboid individuals; I, division; J, O, two stages in cyst-formation. L, *Phacomonas pelagica* Lohmann (after Lohmann), individual viewed from narrow side. M, *Nephrochloris incerta* Geitler (after Geitler), on the left front-view, on the right side-view. *c*, chloroplast; *m*, membrane of cyst; *n*, nucleus; *o*, oil-drops; *v*, contractile vacuole. H, *Botrydiopsis arrhiza* Borzi and K, *Monocilia* sp. (both after Vlk), structure of flagella.

the cells contain bright refractive bodies which are believed to consist of leucosin (p. 508). A contractile vacuole has not been observed.

Pascher's *Chloromeson* ((67) p. 405) has slightly flattened, very amoeboid cells with two very unequal flagella, the long one being as much as seven times the length of the body (fig. 154 G, N). The single chloroplast has the form of a curved band occupying the central part of the protoplast, a position met with also in other forms (cf. *Chlorogloea*, p. 474). *Phacomonas pelagica* (51), a marine planktont, has lenticular individuals with the rather coarse flagella arising from a slight beak (fig. 154 L) and two lateral chloroplasts. Pascher (59) has recorded the same form in freshwater plankton. Its assignation to the Xanthophyceae is scarcely fully established (cf. p. 655).

Other genera show more markedly the dorsiventrality indicated in *Heterochloris*. *Ankylonoton* ((72) p. 306) and *Chlorochromonas* (50), especially the latter, recall the Chrysophycean genus *Ochromonas* (p. 515). The single large chloroplast of the former has a pyrenoid-like body apposed to it. In *Chlorochromonas*, recorded from Lake Mendota in America, the cells have a very delicate periplast showing an oblique emargination at the anterior end, while the posterior extremity is often drawn out into a long filiform pseudopodium by means of which attachment to a substratum can be effected (fig. 154 E). The chloroplasts are small, and a second species described by Gavaudan (27) exhibits abundant holozoic nutrition. *Nephrochloris* (29), another dorsiventral form so far only observed in the mucilage of a planktonic *Anabaena*, has cells with a single thick flagellum inserted a little way beneath the front end (fig. 154 M). The apparently single chloroplast is a broad curved plate occupying the periphery of the protoplast.

The motile unicell is thus not very widely represented among Xanthophyceae, and the relevant forms are seemingly restricted in their occurrence; at present no modifications, other than the colourless and rhizopodial forms already mentioned, are known. The ordinary method of multiplication appears to be by longitudinal division during the motile phase (fig. 154 I); in *Heterochloris* palmelloid stages have also been observed. The resting stages are constituted by cysts which are reported for several genera. In *Chloramoeba* they are ellipsoidal bodies provided with a thick membrane and filled with large oil-globules (fig. 154 F). Those of *Heterochloris* have a silicified wall composed, according to Pascher, of two slightly unequal halves. In *Chloromeson* they are formed endogenously (fig. 154 J) and their verrucose silicified membrane consists of two very unequal pieces (fig. 154 O). In this and other respects this form again approximates closely to some species of *Ochromonas*.

(b) The Palmelloid Forms (Heterocapsineae)

Palmelloid forms are rather more numerous, though the assignation of some of the genera included here is not altogether beyond doubt. A close parallel to *Tetraspora* is constituted by the rare *Chlorosaccus* (53) which occurs attached to freshwater aquatics as pale yellow-green diffluent membranous masses produced into conical protuberances (fig. 155 A). The numerous pyriform cells, with two or more yellow-green parietal chloroplasts (fig. 155 B), are arranged peripherally with the pointed ends outwards within structureless mucilage. The cells multiply by longitudinal division, usually in two planes at right angles to one another, so that many of them are found in groups of fours. Reproduction is effected by typical Xanthophycean swarmers (fig. 155 C) formed directly from the cells of the colony, whilst resting stages are constituted by thick-walled cysts originating from enlarged cells. *Gloeochloris* ((72) p. 319) is apparently similar, but its colonies are free-floating with numerous ellipsoidal cells in a peripheral position.

Gardner's *Leuvenia natans* (26), at present only known from a Californian lake, occurs in the shape of irregular, frayed or reticulate, free-floating mucilage-masses[1] harbouring countless rounded cells (fig. 155 D). The pear-shaped zoospores (fig. 155 E) have two dark green chloroplasts and two unequal flagella, the longer of which is directed forwards, while the shorter trails behind; towards the end of the motile period the swarmers become amoeboid. On coming to rest (fig. 155 I) these swarmers float to the surface of the water, secrete a membrane and undergo considerable enlargement accompanied by division of chloroplasts and nuclei to form a large spherical cell (fig. 155 F, J). The latter may float freely for a time and then either forms further swarmers or by division and the secretion of mucilage presumably gives rise to the palmelloid stages.[1] It appears that the swarmers can also develop into large cysts with a bivalved membrane from which the contents subsequently escape (fig. 155 G). Many features of the life-cycle are still unclear. Both in *Chlorosaccus* and *Leuvenia* the cells in the palmelloid phase are provided with a membrane.

Chlorogloea ((67) p. 407) possesses naked rounded cells embedded in structureless mucilage and containing two (or just after division one) rather small band-shaped chloroplasts which, as in *Chloromeson*, are located near the centre of the protoplast (fig. 155 H). The swarmers that effect reproduction are inadequately known. *Pelagocystis oceanica* Lohmann ((52) p. 49) (including *Clementsia* Murray (56)), found in the plankton of the Atlantic, probably belongs to this series, although its

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[1] According to Smith ((91 a) p. 150) this alga normally occurs as isolated coccoid cells and he therefore includes it in the Heterococcales.

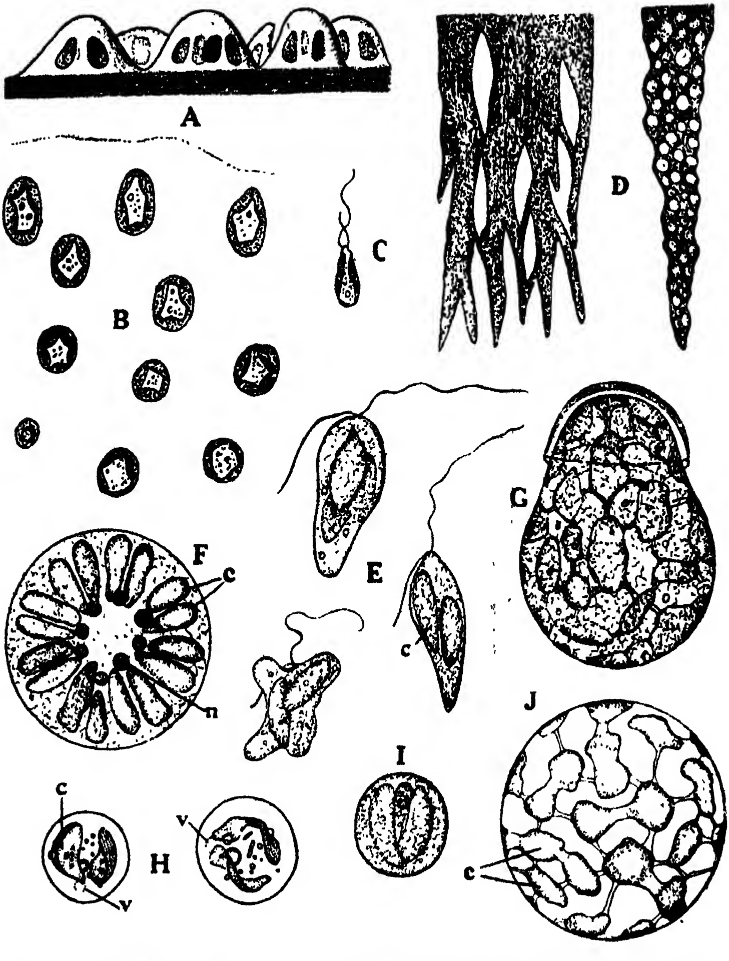

Fig. 155. Heterocapsineae. A–C, *Chlorosaccus fluidus* Luther (after Luther); A, young colonies viewed from the side; B, small part of a colony; C, swarmer. D–G, I, J, *Leuvenia natans* Gardn. (after Gardner); D, palmelloid stage, on the right a part enlarged to show the cells; E, three swarmers, the lowest amoeboid; F, cell in optical section, a pair of chloroplasts to each nucleus; G, cell just escaped from cyst, part of whose membrane is seen at the top; I, resting cell derived from swarmer; J, free-floating cell, chloroplasts connected by cytoplasmic threads. H, *Chlorogloea endochloris* Pascher (after Pascher), two cells. *c*, chloroplast; *n*, nucleus; *v*, contractile vacuole.

motile stages have not yet been observed. The spherical or ellipsoidal cells with a bell-shaped chloroplast are embedded in pairs in varying numbers in mucilage-masses (fig. 156 A) which show more or less clearly the layers belonging to successive generations (cf. *Gloeocystis*).

A more highly developed type is seen in Pascher's *Helminthogloea* ((72) p. 323), only once found in salt-marshes, where the cells are contained in richly branched, rather firm mucilage-strands forming minute upright tufts (about 1 mm. high). Cell-division is more copious near the tips of the branches (cf. *Hydrurus* among Chrysophyceae, p. 546).

Most recent authorities also refer to this series, the common freshwater planktonic alga *Botryococcus* (12, 16, 29)[1] which not infrequently forms water-flowers. The colonies (fig. 156 C) are of very varied shape, being composed of a number of more or less spherical aggregates with radially arranged cells (fig. 156 B, I) embedded within a tough, sometimes orange-coloured mucous envelope which is folded or wrinkled and frequently drawn out into irregular lobes or spine-like processes. Often smaller colonies are united by more or less rigid prolongations of the mucus into larger ones (fig. 156 D). At times the cells can be squeezed out of their envelopes which are so firm that they retain their shape (fig. 156 C).

The tough mucus obscures the cell-structure which is often almost indecipherable. Each cell appears to be lodged within a funnel-shaped mucilage-cup (fig. 156 G, H) which is composed of successive thimble-shaped layers fitting into one another and whose base is prolonged into a thick stalk which extends to the centre of the aggregate (fig. 156 G, I). This structure is, however, only readily recognisable in young stages, since later on the mucilage swells and the details are no longer evident. The origin of the envelope is not clearly established. It appears that in some cases the cells lie at the periphery of the mucilage, whilst in others the latter forms a definite superficial layer; in *B. protuberans* West (103) the cells project prominently. Some of the specially opaque stages were described by the Wests in 1897 (102) under the appropriate name of *Ineffigiata*, whose identity with the common *Botryococcus Braunii* was only later established.

The usually ellipsoid or obovate cells (fig. 156 E, F) possess a thin membrane which, according to Geitler (29), on treatment with dilute sulphuric acid swells and separates into two unequal pieces. The cells contain a single parietal chloroplast, including a naked pyrenoid-like body of doubtful nature and occasionally small granules which have been stated to consist of starch ((16) p. 338). The cells at times harbour abundant oil which in the late summer becomes brick-red[2] owing to the presence of a dissolved pigment (haematochrome?); the oil may escape from the cells and often occurs abundantly in the mucilage

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[1] Including *Botryosphaera* Chodat (18 a).

[2] According to Gams (25) this is characteristic of waters rich in nutriment

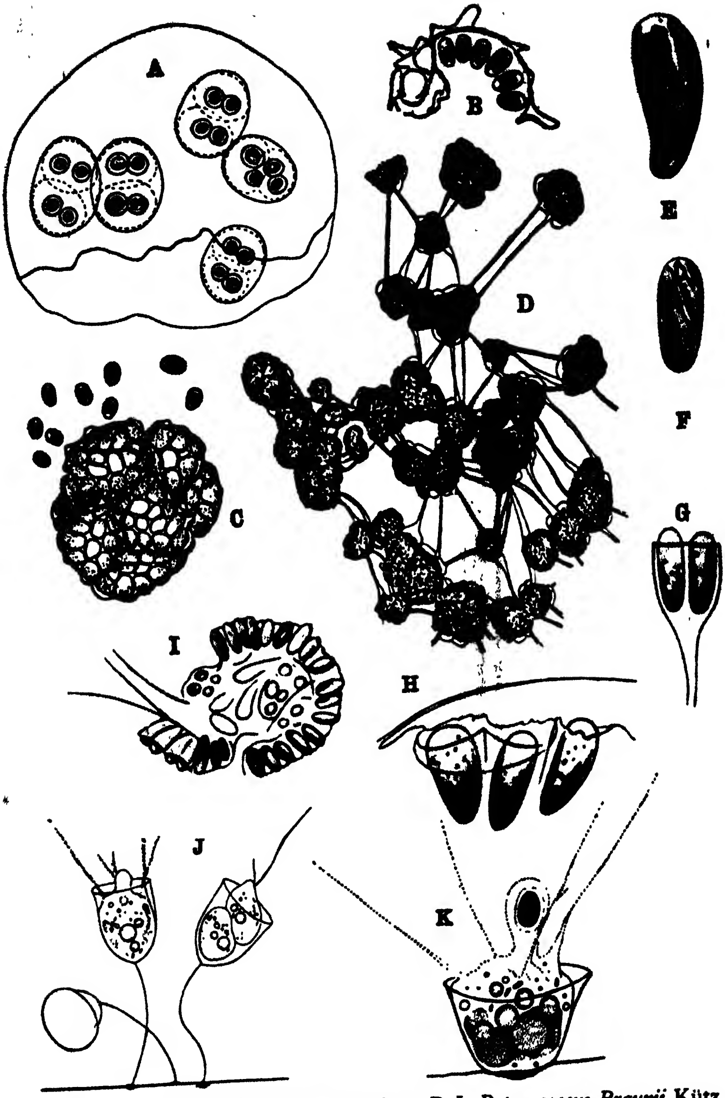

Fig. 156. A, *Pelagocystis oceanica* Lohm. B–I, *Botryococcus Braunii* Kütz.; B, part of colony in section; C, colony from which many of the cells have been squeezed out; D, compound colony; E, F, single cells; G, stalk and cup holding two cells; H, cells in their mucilage-envelopes; I, colony in optical section. J, *Stipitococcus vas* Pascher. K, *Rhizolekane sessilis* Pascher. (A after Lohmann; B, C after West; D after Carlson; J, K after Pascher; the rest after Chodat)

or it adheres to the aggregates and to the processes of the enveloping mucilage. Of great interest is Carlson's record (12) of the presence of short arched pseudocilia arising in a tuft from the outer end of the cell, an observation that requires confirmation.

The cells appear to multiply by longitudinal division only (cf. fig. 156 G), whereby the aggregates increase in size, later to divide into two or more, though for a time usually remaining connected by more or less elongate processes of the envelope. This is the only method of propagation certainly known. The records of swarmers remain doubtful (cf. however (81) p. 387). On the other hand division of the cell-contents into 2–4 aplanospores seems to occur. Although there is much that supports a reference to the Xanthophyceae, the position of *Botryococcus* cannot be said to be certainly established; in particular the reported presence of starch calls for further enquiry.

The deposits formed by this alga are distinguished by their very slow rate of decay and are sometimes responsible for very considerable sapropelic accumulations. Various authorities (4, 94, 107) are of the opinion that the Palaeozoic remains (*Pila*, *Reinschia*) found in boghead coals are ancient allies of *Botryococcus* and that such coals were largely formed by them. This has, however, not met with general agreement (cf. (41), (78), (106)).

(*c*) THE DENDROID FORMS (HETERODENDRINEAE)

The sole representative of the dendroid type is furnished by *Mischococcus* ((8), (10) p. 121, (57), (66) p. 33, (96), (97)), a freshwater epiphyte apparently restricted to calcareous waters. *M. confervicola* Naeg. frequently shows more or less regular subdichotomous branching of the mucilage-stalks bearing the rounded cells (fig. 157 C), though numerous irregularities occur. Reproduction is usually effected by swarmers which appear to have but a single anterior flagellum (fig. 157 F), although for another species Vischer (98) records two unequal flagella. On coming to rest the zoospores give rise to a spherical cell attached by a small mucilage-cushion (fig. 157 A, *a*). Sooner or later the upper part of the membrane of this cell either gelatinises or becomes detached as a lid, whereupon the protoplast shifts to the aperture and becomes enveloped by a new membrane (cf. fig. 157 B). Subsequently this cell secretes at its base a cylinder of mucilage (*m*) which gradually carries it aloft, the original membrane appearing as a small nodose swelling at the base. The protoplast may then divide transversely and the two daughter-protoplasts be carried up by a fresh stalk in the same way. Sooner or later division takes place along another plane (longitudinal?), the two resulting protoplasts, after rupture of the parent-membrane, being carried up on a common mucilage-stalk; when the daughter-cells in their turn divide each group forms a separate stalk, so that a first dichotomy is initiated. If this series of events be continued, the regular forked colonies are formed.

It seems, however, that in many cases division is transverse, only one of the two daughter-protoplasts shifting to the aperture, this cell then gradually becoming separated from its sister by the secretion of an intervening mucilage-stalk (cf. fig. 157 B). In this way short chains of cells may be formed, as frequently occurs in the later growth

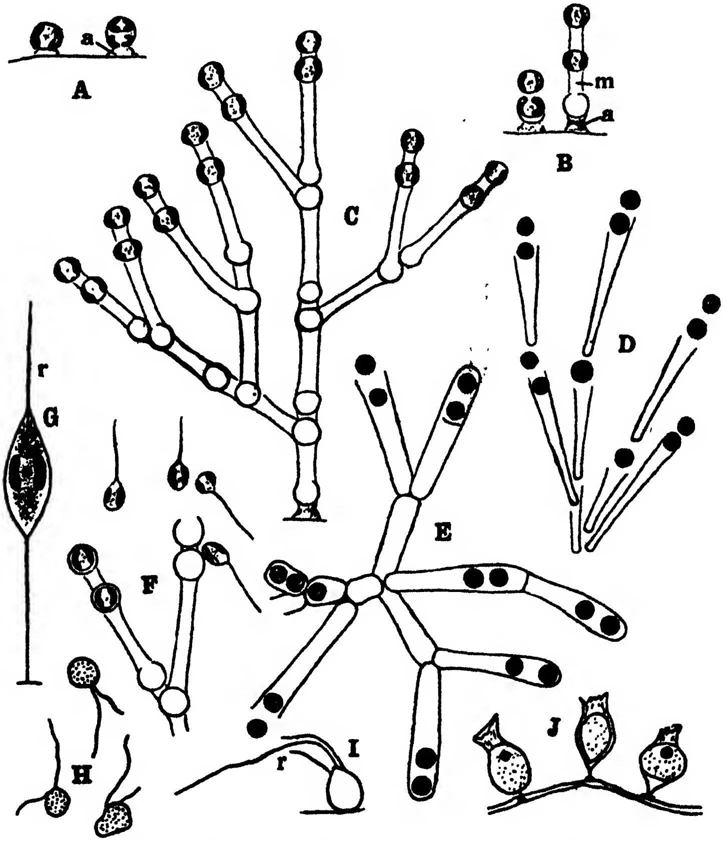

Fig. 157. A–F, *Mischococcus confervicola* Naeg.; A, B, young stages; C–E, diverse forms of colonies; F, swarmer-formation. G, *Stipitococcus Lauterbornei* Schmidle. H–J, *S. urceolatus* West; H, swarmers; I, cell with rhizopodia; J, habit. *a*, attaching cushion; *m*, mucilage; *r*, rhizopodium. (A–C, F after Borzi; D, E after West; G after Schmidle; the rest after Poulton.)

of the colony (fig. 157 C). Moreover, division into four is not infrequent, in which case four stalks may be seen originating from the same point (fig. 157 E). The mucilage-stalks are as wide as, or even wider than, the cells producing them (fig. 157 D, E), although in preserved material which has often been figured (as in fig. 157 A–C) the stalks shrink so that they appear much narrower.

The cells have a delicate membrane and contain two (rarely four) parietal chloroplasts. The swarmers have prominent eye-spots and appear usually to be formed singly or in twos within the cells, although Vischer records the formation of as many as 16 per cell; aplanospores are frequent and are sometimes produced to the number of four or eight. Multiplication may apparently also be effected by the detachment of cells from older colonies. Sexual reproduction has been recorded ((10) p. 135), but remains doubtful; the zygote is stated to give rise to an epiphytic cushion-like palmelloid stage.

The type of colony is clearly comparable to that of the Chlorodendrineae among Volvocales. There appears, however, to be a greater variability and Pascher ((66) p. 35), Virieux (96), and Vischer (97, 98) record diverse abnormal states. According to the last the typical dendroid colonies are formed only when nutriment is scanty and especially when nitrogen is deficient. In nutritive solutions masses of coccoid cells are alone produced. Addition of glucose and strong light favour the development of the mucilage-stalks.

(*d*) THE RHIZOPODIAL FORMS (HETERORHIZIDINEAE)

The little known genus *Stipitococcus* (89, 101) represents a fourth line of development among the Heterochloridales, for which there is at present no parallel among Chlorophyceae, although equivalent forms occur in the Chrysophyceae (p. 532). The small protoplasts are enclosed in a variously shaped envelope which is often attached by an extremely fine stalk (figs. 156 J, 157 G) to filamentous Algae; in *S. urceolatus* Poulton ((80) p. 6) states that there is a delicate cell-wall which appears doubtful. The protoplast contains a single chloroplast and is produced apically into one or more, sometimes long rhizopodial threads (fig. 157 G, I, *r*). Multiplication is effected by swarmers (fig. 157 H), but the statement that the flagellum constitutes the stalk (89) is open to doubt.

Stipitococcus urceolatus (fig. 157 J), the first species of the genus to be described (101), has been suspected of being a member of the Chrysophyceae. Judging by Poulton's account (80) it possesses an exceedingly reduced chromatophore, but the reaction with hydrochloric acid and the swarmers make it probable that this form should be referred to the Xanthophyceae, to which Pascher's *S. vas* ((72) p. 318) (fig. 156 J) undoubtedly belongs. Pascher (72) has described a somewhat different type under the name of *Rhizolekane*. This rhizopodial form lives within a sessile, cup-shaped envelope (fig. 156 K) and constitutes a close parallel to *Rhizaster* among Chrysophyceae (p. 536). It exhibits holozoic nutrition, although it possesses a well-defined chloroplast.

Order II. *HETEROCOCCALES*

These are the coccoid forms among the Xanthophyceae and are parallel to the Chlorococcales among Chlorophyceae. In part they are so similar to members of the Chlorococcales that, prior to the clear recognition of the differences between the two classes, many were referred to genera of that order. The Heterococcales, however, possess the characteristic chloroplasts, oil as the product of assimilation, and in many cases reproduce by typical swarmers with two unequal flagella. There is need to emphasise these facts, since the degree of similarity of outward form is in part astounding. Apart from the ordinary spherical type, such as *Chlorobotrys* (fig. 159 A) which was first described as a species of *Chlorococcum*, we have *Botrydiopsis* (fig. 158 H) much resembling a small yellow-green *Eremosphaera*, *Acanthochloris* (fig. 158 P) parallel to *Trochiscia*, *Characiopsis* (fig. 160 A, B) so similar to *Characium* that its species were long included in the latter, and Pascher's *Tetraëdriella* (fig. 159 G, H), etc., closely parallel to *Tetraëdron*. The analogy goes further (65), since one can distinguish a set of forms (*Chlorobotrys*, *Centritractus*), which appear to be azoosporic, from a set in which swarmers are the rule (e.g. *Characiopsis*, *Halosphaera*).

It does not appear that this order has adapted itself so strikingly to a planktonic existence as have the Chlorococcales, although *Pseudotetraëdron* (fig. 159 P) and *Centritractus* (fig. 159 Q) represent freshwater planktonic types, while the two common oceanic plankton forms, *Halosphaera* and *Meringosphaera*, are now recognised as members of the Heterococcales. Perhaps one of the most striking differences in comparing the latter with the Chlorococcales is the complete absence of differentiated colonial types in the Heterococcales,[1] a feature which corresponds to their absence among Heterochloridales.

THE ZOOSPORIC FORMS (HALOSPHAERACEAE)

Among the free-floating Heterococcales we may consider first those in which formation of zoospores is the rule. *Halosphaera viridis* Schmitz (35, 58, 62, 90) occurs as a planktont in all warmer seas and is found in spring over the whole area of the North Atlantic (74),

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[1] Pascher ((66) p. 39), however, regards *Botryococcus* and its allies as colonial members of Heterococcales.

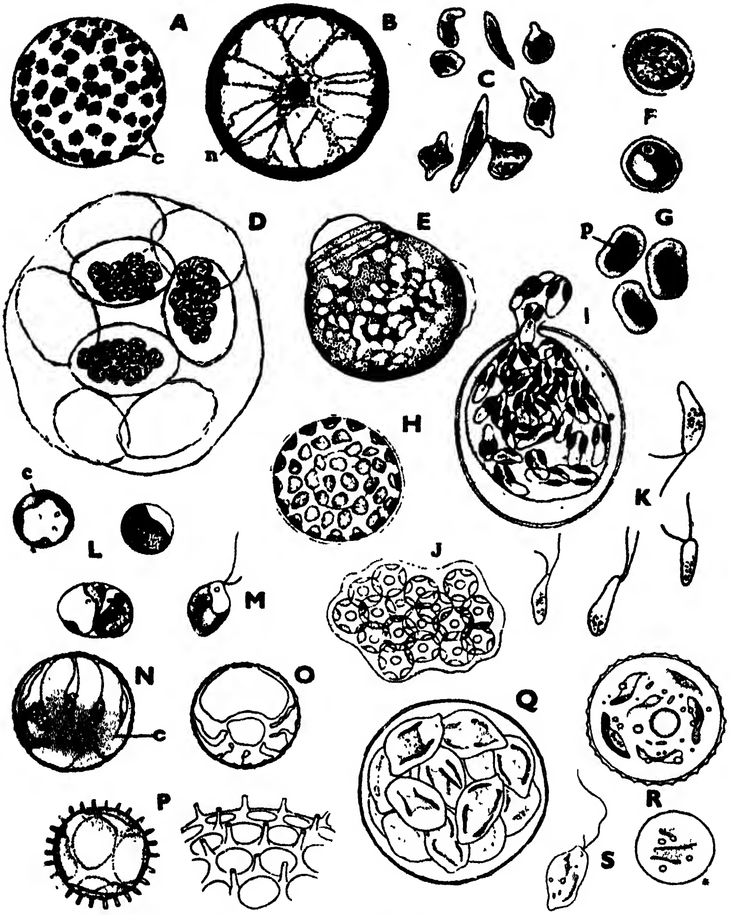

Fig. 158. Heterococcales. A–F, *Halosphaera viridis* Schmitz; A, mature cell in surface-view; B, young cell in optical section; C, amoeboid spores; D, mature cell with aplanospores; E, exuviation of the membrane; F, young cells (?). G–J, *Botrydiopsis arrhiza* Borzi; G, chloroplasts with pyrenoids (*p*); H, vegetative cell; I, liberation of swarmers; J, aplanospore-formation. K, *B. minor* Chod., swarmers. L, M, *Pleurochloris commutata* Pascher; L, three cells, the lowest dividing; M, swarmer. N, O, *Arachnochloris major* Pascher; N, surface-view; O, diagram of section of cell. P, *Acanthochloris brevispinosa* Pascher, on the right a piece of cell-wall enlarged. Q–S, *Endochloridion polychloron* Pascher; Q, swarmer-formation; R, two cells, the lower just produced from a swarmer; S, swarmer. *c*, chloroplast; *n*, nucleus. (A–D after Ostenfeld; E after Gran; F after Schiller; G after Korschikoff; H–J after Borzi; K after Chodat; the rest after Pascher.)

apparently carried there by the Gulf Stream. The large spherical cells (fig. 158 A, B) contain a single nucleus (*n*) which is either suspended in the central vacuole or lodged in the parietal cytoplasm. There are numerous parietal, yellow-green chloroplasts (*c*) which are discoid and somewhat angular and in the young cells are joined by cytoplasmic threads to form a network. The membrane is largely composed of pectic substances and harbours a certain amount of silica; it consists of two equal halves which are joined at their margins. As the cell enlarges, new membranes are formed internal to the previous ones, the older ones rupturing into their two halves which may remain clinging to the cell for some time (fig. 158 E).

The freshwater *Botrydiopsis* ((10) p. 169, (21)), which is apparently also a common soil alga (55), is so similar to *Halosphaera*, except for the smaller size of its cells (fig. 158 H), that an inclusion of its species in *Halosphaera* has often been advocated (62). The presence of naked pyrenoids in the chloroplasts of *B. arrhiza* (fig. 158 G) has been recorded by Korschikoff (45).[1]

A somewhat different type is seen in *Pleurochloris* (fig. 158 L), recorded by Pascher ((66) p. 46) from damp soil (cf. also (76)). Here the minute cells usually contain but a single parietal chloroplast occupying a large part of the periphery of the protoplast, so that there is appreciable resemblance to a *Chlorococcum*. Another striking form recently described by Pascher ((67) p. 409) is *Arachnochloris* (fig. 158 N, O), with large spherical or ellipsoidal cells whose thin silicified membrane is provided with a network of small rounded depressions. The single elaborate chloroplast consists of a thickened central mass produced into long parietal band-shaped lobes towards the one side and into much shorter ones on the other. *Endochloridion* ((67) p. 415) has a similar membrane, but the cells contain one or several chloroplasts having the same subcentral position (fig. 158 R) as in *Chloromeson* and *Chlorogloea*. In *Acanthochloris* ((67) p. 418) the membrane is composed of the usual two pieces and is produced into spines between the depressions (fig. 158 P).

In all of these genera swarmers, usually produced in considerable numbers in the cells (fig. 158 I, Q), have been recorded; in *Arachnochloris*, however, they appear to be formed only in pairs. The characteristic features of the swarmers will be sufficiently apparent from the figures (fig. 158 K, M, S). Those of *Halosphaera*[2] are oval or spherical, possess a pair of lateral chloroplasts and an eye-spot and

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[1] Petrová (77) is of the opinion that *Botrydiopsis minor* Chodat (18) is one of the Chlorophyceae allied to *Dictyococcus*. According to investigations carried out by Miss James in my laboratory there is an undoubted Xanthophycean alga which corresponds to Chodat's *B. minor* and Petrová's conclusions are likely to be due to confusion with a very similar green form.

[2] The swarmers described and figured by Schmitz (90) are certainly not typical.

exhibit some metaboly (22) (fig. 158 C). In practically all cases, however, aplanospores can replace the swarmers (cf. fig. 158 D, J) and these aplanospores often develop as autospores, acquiring all the characteristics of the mature cells before liberation. In *Halosphaera* the aplanospores (30) are stated to have a silicified membrane composed of two halves (62). According to Borzi (10) the aplanospores of *Botrydiopsis arrhiza* become thick-walled resting hypnospores which later produce gametes, an observation which has to some extent been confirmed by Dangeard (21). In *Halosphaera* there are also known resting stages formed by contraction of the protoplast into a single spore provided with a thick bipartite membrane (62); similar structures have been observed in *Botrydiopsis*.

Despite its abundance the life-history of *Halosphaera* is imperfectly known and the development of the mature cells from the swarmers has not been observed. Schiller (88) records from the Adriatic the appearance of small cells with a thick mucilage-envelope (fig. 158 F) some considerable time before the larger individuals occur in the plankton, but it remains doubtful whether these belong to the same organism.

THE AZOOSPORIC UNATTACHED FORMS (CHLOROBOTRYDACEAE)

The best known of these is *Chlorobotrys regularis* ((7), (72) p. 329, (102)) whose spherical cells (fig. 159 A) are not uncommon in the waters of bogs. The cells occur isolated or more commonly in families of 2–16 surrounded by a wide homogeneous mucilage-envelope (fig. 159 D). The cell-walls are often of some thickness and prominently silicified. The discoid parietal chloroplasts are sometimes few, sometimes many (fig. 159 A, D), and one or more red pigment-spots are commonly found in the cells. *Monodus* (18, 76) is distinguished by the shape of its cells (fig. 159 E, F) which are asymmetric and often pointed at one end.

Tetraëdriella (fig. 159 G, H), *Tetragoniella* (fig. 159 J, K), and other allied forms described by Pascher (67) are clearly Xanthophycean parallels of the green *Tetraëdron*, with cells of characteristic shape and more or less numerous chloroplasts. Some species of *Tetraëdriella* are marine ((73) p. 199). Geitler's *Goniochloris* (30, 67), with markedly flattened cells (fig. 159 L, M), shows a certain degree of convergence to *Triceratium* among the Bacillariophyceae (cf. p. 569).

Other forms show definite planktonic adaptations. *Meringosphaera* (51, 64, 73, 87), with several species widely distributed in marine plankton, has cells of diverse shapes (spherical, ellipsoidal, tetrahedral, etc.) which sometimes possess a mucilage-envelope and bear on their surface a number of colourless bristles which are either straight or undulated (fig. 159 N, O); in some species these are uniformly distributed around the periphery of the cell, in others they

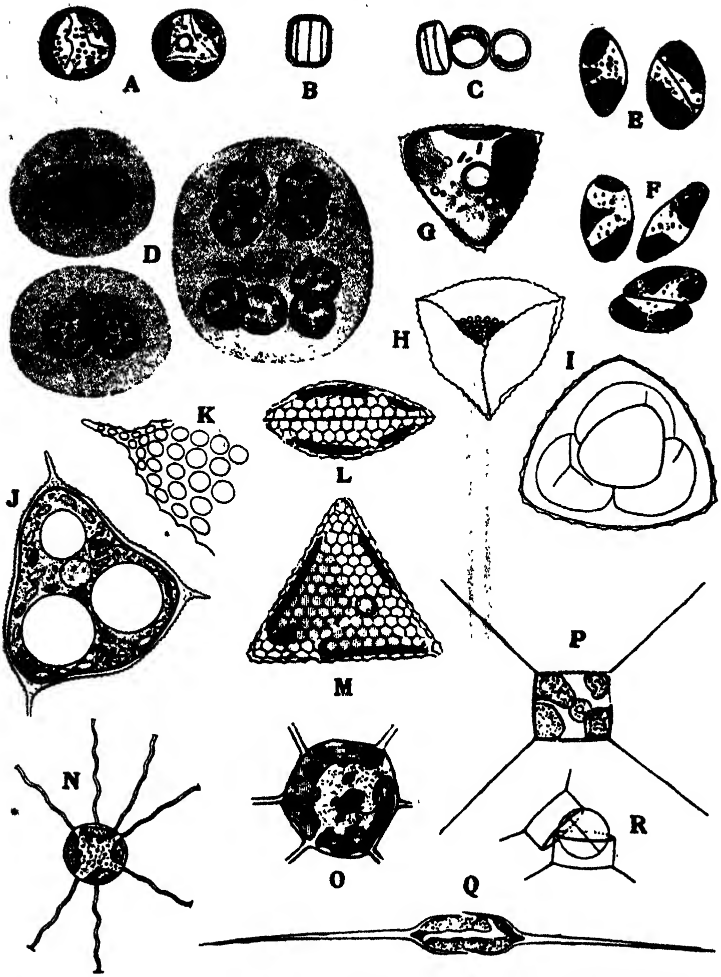

Fig. 159. Heterococcales. A–D, *Chlorobotrys regularis* (West) Bohl.; A, ordinary cells; B, cyst; C, germination of same; D, colonies. E, F, *Monodus subterraneus* Petersen. G–I, *Tetraëdriella acuta* Pascher; G, optical section; H, membrane-structure; I, autospore-formation. J, K, *Tetragoniella gigas* Pascher; K, part of membrane. L, M, *Goniochloris sculpta* Geitler; L, side- and M, front-view. N, O, *Meringosphaera mediterranea* Lohm.; O, optical section. P, R, *Pseudotetraëdron neglectum* Pascher; R, aplanospore. Q, *Centritractus belonophorus* (Schmidle) Lemm. (A–C after Bohlin; D after West; E, F after Petersen; L, M after Geitler; N after Lohmann; O after Schiller; Q after Schmidle; the rest after Pascher.)

are confined to one side. Both the cell-wall and the bristles contain silica. In *M. mediterranea* the membrane consists of two halves (105). A more specialised type is seen in *Schilleriella* ((73) p. 216), where three bristles of unequal length arise at one end.

In *Centritractus* (48) and *Pseudotetraëdron* (61), two freshwater plankton-forms, the cell-walls are distinctly composed of two halves, a feature which is not yet established for *Chlorobotrys*, most species of *Meringosphaera*, etc., although probable on comparative grounds. The cells of *Centritractus* (fig. 159 Q) are cylindrical and prolonged at each end into a long pointed spine, whilst in *Pseudotetraëdron* (fig. 159 P) they are flattened, elliptical in cross-section, and produced at the four corners into long delicate bristles.

The majority of these forms appear to reproduce by aplanospores often developed as autospores (fig. 159 I), although swarmers occur in *Tetragoniella* and *Goniochloris*,[1] while Poulton ((79) p. 321) records zoospores in a species of *Chlorobotrys*, as yet only known from cultures and probably not belonging to this genus (cf. also (72) p. 333). Several of these genera form endogenous bivalved silicified cysts; those of *Chlorobotrys* (fig. 159 B) have the shape of flat cylinders and on germination produce two aplanospores (fig. 159 C).

THE EPIPHYTIC HETEROCOCCALES

The epiphytic Heterococcales are grouped in the family Chlorotheciaceae, of which *Characiopsis* ((10) p. 151, (13), (14), (49)) is the most widely distributed genus. The cells, which are solitary or gregarious, vary in shape in the different species (cf. fig. 160 A–D) and are generally provided with a short thick stalk attached by a basal mucilage-cushion. According to Pascher ((66) p. 57) the membrane is composed of two, usually unequal pieces of which the upper is the smaller and becomes detached when swarmers are liberated; in certain species the upper piece is thickened and may be coloured reddish brown by iron compounds (fig. 160 F). Some species possess but a single chloroplast, although most have a number of discoid ones (fig. 160 A–D). According to Carter (13) the chloroplasts of some species are only clearly distinguishable in the young cells, nearly the whole of the peripheral cytoplasm appearing pigmented in the older ones. The mature cells are often multinucleate (fig. 160 C, D), a condition that probably precedes zoospore-formation. In *Peroniella* (34, 91) the spherical or ellipsoidal cells are seated at the end of a long hyaline stalk (fig. 160 E).

Chlorothecium ((9), (10) p. 139) chiefly differs from *Characiopsis* in

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[1] This shows that, as in the Chlorococcales (p. 147), a sharp distinction into zoosporic and azoosporic forms is not possible.

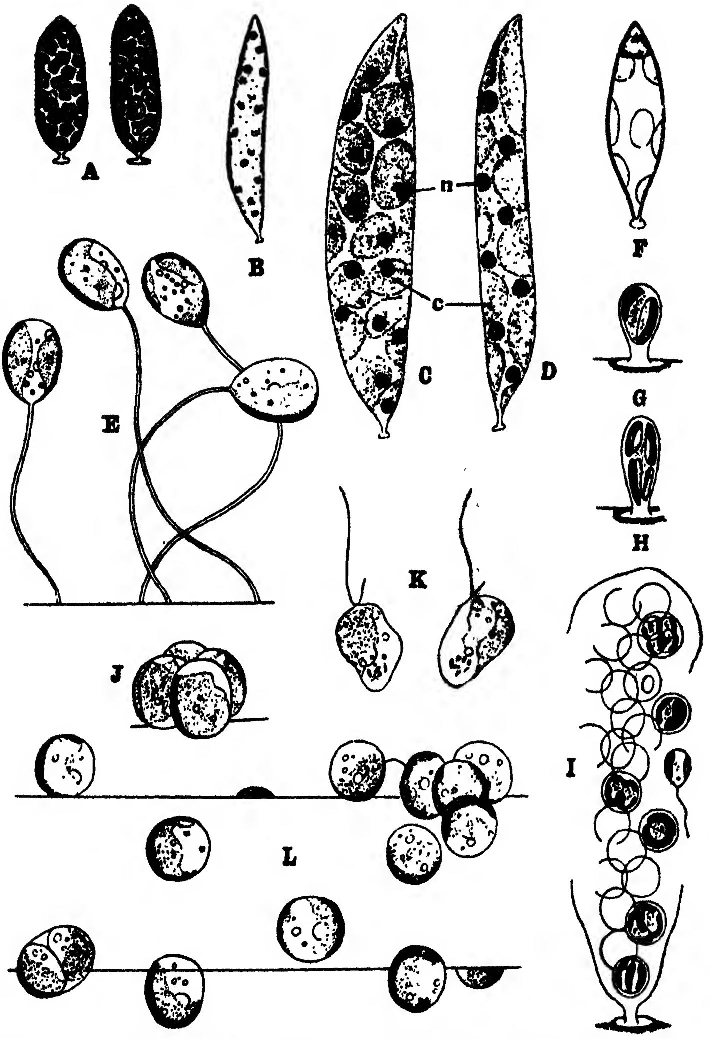

Fig. 160. Epiphytic Heterococcales. A, *Characiopsis turgida* West. B–D, *C. saccata* Carter; C, probable swarmer-formation; D, with chloroplasts (*c*) and nuclei (*n*). E, *Peroniella curvipes* Pascher. F, *Characiopsis crassiapex* Printz. G–I, *Chlorothecium Pirottae* Borzi; G, H, vegetative cells; I, liberation of aplanospores and escape of swarmers from same. J–L, *Lutherella adhaerens* Pascher; J, formation of autospores; K, swarmers; L, habit. (A after West; B–D after Carter; G–I after Borzi; the rest after Pascher.)

the broad attachment (fig. 160 H) and in the fact that the two halves of the membrane are nearly equal (cf. fig. 160 I). A peculiar epiphyte, recently described by Pascher ((67) p. 442) under the name of *Lutherella* (fig. 160 J, L), shows a considerable degree of parallel to *Epichrysis* among the Chrysophyceae (p. 548). The rounded sessile cells contain a single parietal chloroplast.

Most Chlorotheciaceae normally reproduce by zoospores, usually formed in considerable numbers in the cells (fig. 160 I), although in *Lutherella* (fig. 160 K) they are produced in pairs.[1] In *Characiopsis* thick-walled aplanospores are known and, according to Borzi ((10) p. 160), such structures can give rise to motile gametes, an observation that requires confirmation. *Chlorothecium* (fig. 160 I) reproduces by 4–16 aplanospores with a bivalved membrane which are liberated by the separation of the two halves of the wall. From these spores 2–4 swarmers with two lateral chloroplasts are set free and these, according to Borzi ((10) p. 145), can again act as gametes.

The multinucleate habit among the Chlorococcales finds its parallel in *Ophiocytium* (Ophiocytiaceae), an abundant freshwater form having the shape of a more or less elongate cylinder, usually somewhat curved and often even spirally wound (fig. 161 A), whilst one or both ends (fig. 161 D) are provided with a spine-like process. Many species are epiphytic and in that case attachment is effected by a knob-like expansion at the end of one of these processes (fig. 161 C). The membrane consists of two very unequal pieces which are clearly distinguishable after treatment with potash (5). There is a small structureless lid (fig. 161 B, F, *l*), the pointed edge of which fits over the elongated basal portion which is composed of a series of strata, each resembling a long thimble with a strongly thickened rim. By apposition of successive strata both thickening of the wall and growth in length of the whole cell are brought about (cf. fig. 161 B). The mature cells always contain several nuclei and a number of chloroplasts, commonly appearing H-shaped in optical section (fig. 161 A).

Reproduction ((66) p. 72, (82)) is effected by zoospores (fig. 161 I, J) or aplanospores (fig. 161 C, H) which are liberated by the detachment of the lid, as a result of swelling of the inner layers of the membrane. At the commencement of swarmer-formation the outlines of the chloroplasts become indistinct. The swarmers, of which there are usually four (rarely eight), lie in a single row and escape with their posterior end foremost. They possess two unequal flagella, one or two chloroplasts, a brown eye-spot, and a basal whitish glistening mass ((66) p. 72). As these swarmers come to rest they become amoeboid and gradually assume a spherical form, whilst the process develops from the glistening mass at the base. In the epiphytic

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[1] In *Characiopsis* the swarmers of several species are stated to possess but a single flagellum.

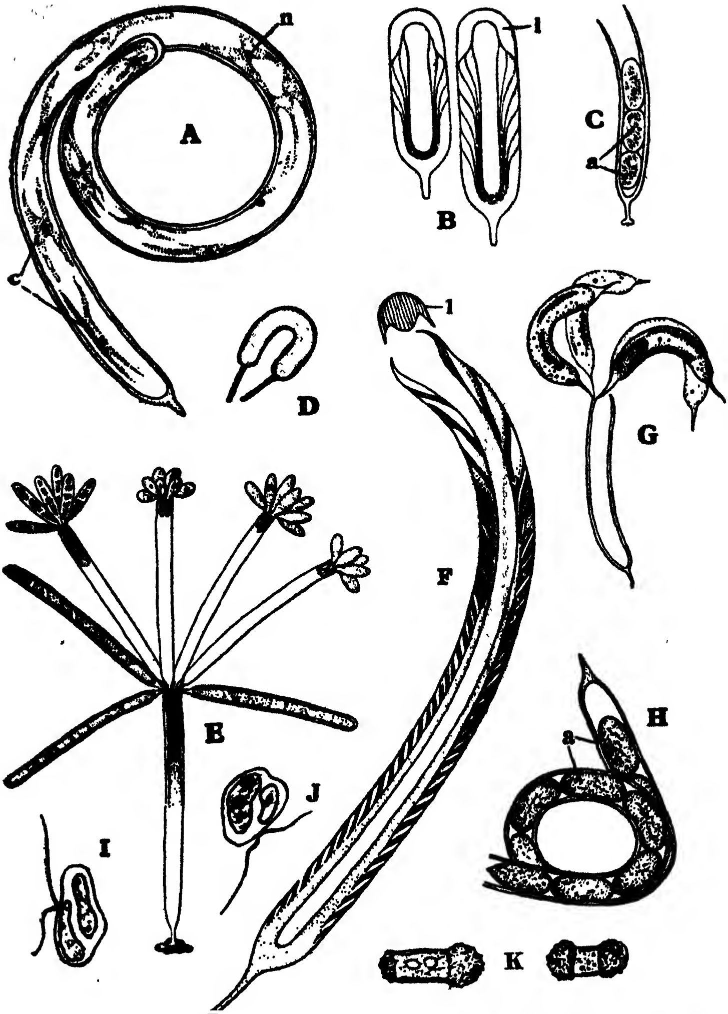

Fig. 161. *Ophiocytium.* A, *O. variabile* Bohl. B, diagrammatic representation of structure of membrane. C, H, *O. cochleare* (Eichw.) A. Br., aplanospores. D, *O. bicuspidatum* (Borge) Lemm. forma *longispina* Lemm. E, *O. arbuscula* A. Br., dendroid colony. F, membrane after treatment with potash. G, *O. cochleare* forma *bicuspidata* Borge, colony-development. I, J, *O. majus* Naeg., swarmers. K, cysts. *a*, aplanospores; *c*, chloroplasts; *l*, lid of membrane; *n*, nuclei. (D after West; E after Braun; I, J after Pröbst; K after Scherffel; the rest after Bohlin.)

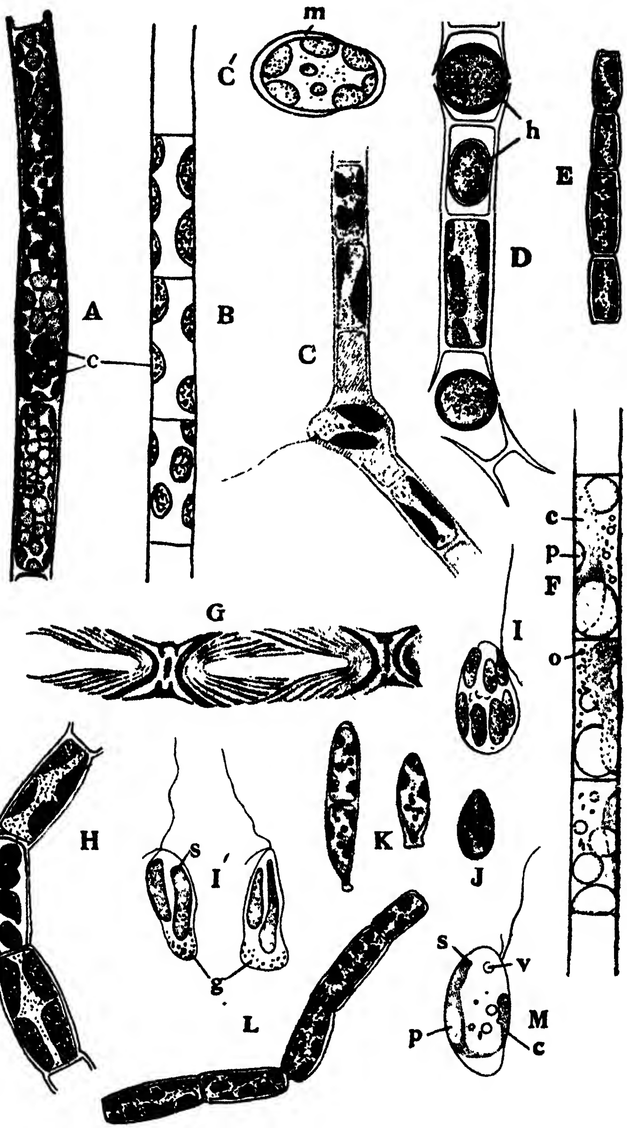

Fig. 162. A, G, I–K, *Tribonema bombycinum* (Ag.) Derb. et Sol.; G, membrane after treatment with potash; I, zoospore; J, K, young plants. B, *T. vulgare*

species therefore attachment is effected by the posterior end. In some species the aplanospores may develop the characteristic process and other features of the mature individual before liberation (autospore-formation (81)).

In several species of *Ophiocytium* (formerly grouped in the genus *Sciadium*) the zoospores settle down at the rim of the parent-individual and there develop into adult cells (fig. 161 G). If this be repeated, dendroid colonies (fig. 161 E) originate, in which the living cells are found only on the ultimate branches (cf. with *Ankistrodesmus*, p. 163).

Pascher (66), on the authority of Scherffel, also records resting spores with a thick, two-valved, often reddish brown wall (fig. 161 K). The occurrence of sexual reproduction is doubtful. *Ophiocytium* is probably to be regarded as a special development of forms like *Characiopsis* with which it shares the inequality in the two halves of the wall and in some cases the multinucleate habit. Many species are no doubt primarily epiphytic, although they readily become detached from their substratum and then continue life as free-floating forms. Species of the genus are known to be capable of existing in waters containing much organic substance and little free oxygen (66).

Order III. *HETEROTRICHALES*

The limited development of the Xanthophyceae in comparison with the Chlorophyceae is very markedly evident in the scanty representation of the filamentous forms. The only frequent type is *Tribonema*[1] (*Conferva* in part), which superficially resembles some species of *Microspora* (p. 208) with which it is often associated in nature and with which it was long confused (46). The unbranched threads are composed of uniform cylindrical or barrel-shaped cells whose wall consists of two equal slightly overlapping halves, so that the filaments have open ends (fig. 162 B, F) and tend to dissociate into H-shaped pieces (fig. 162 D), as in some *Microsporas*; this is, however, the only resemblance, since all the other characteristics of *Tribonema* are

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[1] See (23), (28), (36), (42), (66).

Pascher. C′, *Tribonema* sp., cyst. C, D, *T. minus* West; C, liberation of swarmer; D, hypnospore-formation. E, H, L, *Heterothrix exilis* (Klebs) Pascher; in H the middle cell shows swarmer-formation. F, M, *Tribonema pyrenigerum* Pascher; M, swarmer. I′, *Tribonema* sp., zoospores. *c*, chloroplast; *g*, granules at posterior end of swarmer; *h*, hypnospore; *m*, membrane of cyst; *o*, oil; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (A, C, D, J, K after West; E, H, L after Bristol; G after Bohlin; I′ after Luther; the rest after Pascher.)

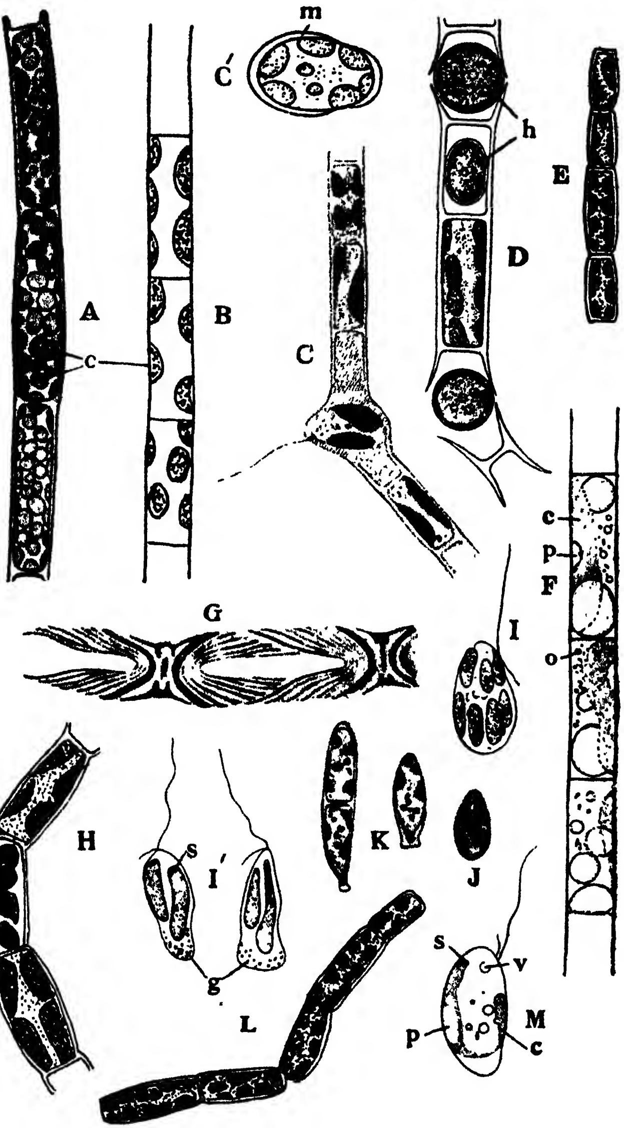

Fig. 162. A, G, I–K, *Tribonema bombycinum* (Ag.) Derb. et Sol.; G, membrane after treatment with potash; I, zoospore; J, K, young plants. B, *T. vulgare*

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typically those of the Xanthophyceae. Bohlin (5) showed that the two halves of a *Tribonema*-cell are directly comparable to those of an *Ophiocytium*-individual, but in the former case they are equal and the strata are devoid of the thickened rim (fig. 162 G). In cell-division a new H-piece arises in the equatorial region, after which the two halves of the parent-cell gradually separate (cf. Desmids).

The cells usually contain a single nucleus, but sometimes two or several are present and, according to Hawlitschka (36), the number of nuclei is characteristic of the species. There are generally a number of parietal chloroplasts which are either relatively few (fig. 162 B) and then often irregular in shape, or more often numerous and discoid (fig. 162 A). In *T. pyrenigerum* ((72) p. 339) there is only a single large chloroplast with a pyrenoid apposed to its inner surface (fig. 162 F).

In the immediate neighbourhood of the nucleus are one, or sometimes two, irregular, highly refractive granules of unknown nature ((66) p. 95). Pascher also records leucosin as frequently occurring in the form of whitish, glistening, rounded masses. Minute globules containing tannin, which have been likened to the fucosan-vesicles of Phaeophyceae, are often present in the cytoplasm, both here and in *Ophiocytium* (15).

Asexual reproduction takes place by means of zoospores (fig. 162 I, M) formed singly or in twos in the ordinary cells and liberated by separation of the two halves of the membrane (fig. 162 C). The two unequal flagella are inserted a little to one side of the apex in a slight depression, while the body of the swarmer is flattened. A pair of contractile vacuoles and a stigma are mostly recognisable (fig. 162 M). The zoospores show marked metaboly (cf. fig. 162 I′) and at times shed their flagella and exhibit amoeboid movement. According to Scherffel ((66) p. 97; cf. also (36) p. 22) cells about to produce zoospores show a marked increase in the highly refractive granules above referred to and, after liberation of the swarmer, these collect especially at the posterior end (fig. 162 I′, *g*). On coming to rest the swarmer elongates, while the posterior end becomes drawn out into a process by means of which attachment is effected (fig. 162 J, K). Some of the granules are then excreted and may be concerned in producing the short stalk. The young germlings are very similar to certain species of *Characiopsis*. There is some evidence that in certain species attachment is effected by the anterior end, but this requires confirmation.

In place of the zoospores there may be formation of aplanospores or hypnospores (fig. 162 D) with a membrane which consists of two unequal pieces (66) (fig. 162 C′). Apparently such aplanospores can, after liberation, either grow direct into a new thread or set free one or two swarmers. Akinetes, which are formed by marked thickening of the membrane and which often assume irregular shapes, are also known.

Sexual reproduction has only once been observed ((85) p. 149). The gametes are described as being morphologically alike, but one comes to rest and rounds off before the other active gamete fuses with it. The more or less spherical zygospores contain a large central mass of leucosin.

Threads of *Tribonema* are occasionally found densely covered with irregular masses of mucilage coloured yellow or brown by ferric carbonate and due to special iron-bacteria which are believed to live in symbiosis with the alga (19). The *Tribonema* is supposed to profit from the symbiosis by the accumulation of carbonate acting as a local buffer by means of which the *p*H of the surrounding water is regulated (95), while the bacteria obtain a supply of oxygen from the alga. A similar association with iron-bacteria is also met with in the case of Green Algae (*Oedogonium*, etc.)

Bumilleria ((10) p. 185, (72) p. 340) has unbranched, unattached threads which are commonly short as a result of abundant fragmentation. The limits of the genus are not altogether clear. According to Pascher (72) in the typical species the membrane of the ordinary cells is not evidently bipartite, although it separates into two halves when swarmers are to be liberated (fig. 163 C), as well as during growth in length of the threads. At these times the cells divide into two or four, the two halves of the parent-membrane appearing as coarse H-pieces (fig. 163 A, B) limiting the short rows of thin-walled cells formed by division and giving an appearance analogous to that of *Binuclearia* (p. 206). At the H-pieces the threads readily break.

Longitudinal division of the cells also occurs, but this appears always to precede rounding off and separation (fig. 163 D). The cell-contents are similar to those of *Tribonema* with which there is also much resemblance in reproduction. Korschikoff (45) has demonstrated the presence of naked pyrenoids situated close to the inner surfaces of the chloroplasts of *B. sicula* (fig. 163 E, H).

Klebs' *Bumilleria exilis* (42), which appears to be a common soil alga (11) showing abundant fragmentation, does not apparently grow in the manner above described, since it lacks the occasional H-pieces of the true *Bumillerias*. Pascher ((72) p. 344) regards it as a separate genus, *Heterothrix* (fig. 162 E, H, L). The same authority has pointed out that the form described by West ((100) p. 258) as *Bumilleria pumila* is quite distinct, constituting a parallel to *Geminella* among Ulotrichales in the possession of a mucilage-sheath around the threads. He establishes it as a fourth genus of Tribonemaceae under the name of *Neonema*.

Few branched members of the Heterotrichales are at present known, viz. *Monocilia* ((33), (72) p. 352) (*Heterococcus* Chodat (17), (18)), *Aeronemum*, and *Heterodendron*, which are classed by Pascher as Heterocloniaceae. The first of these has hitherto mainly been observed in

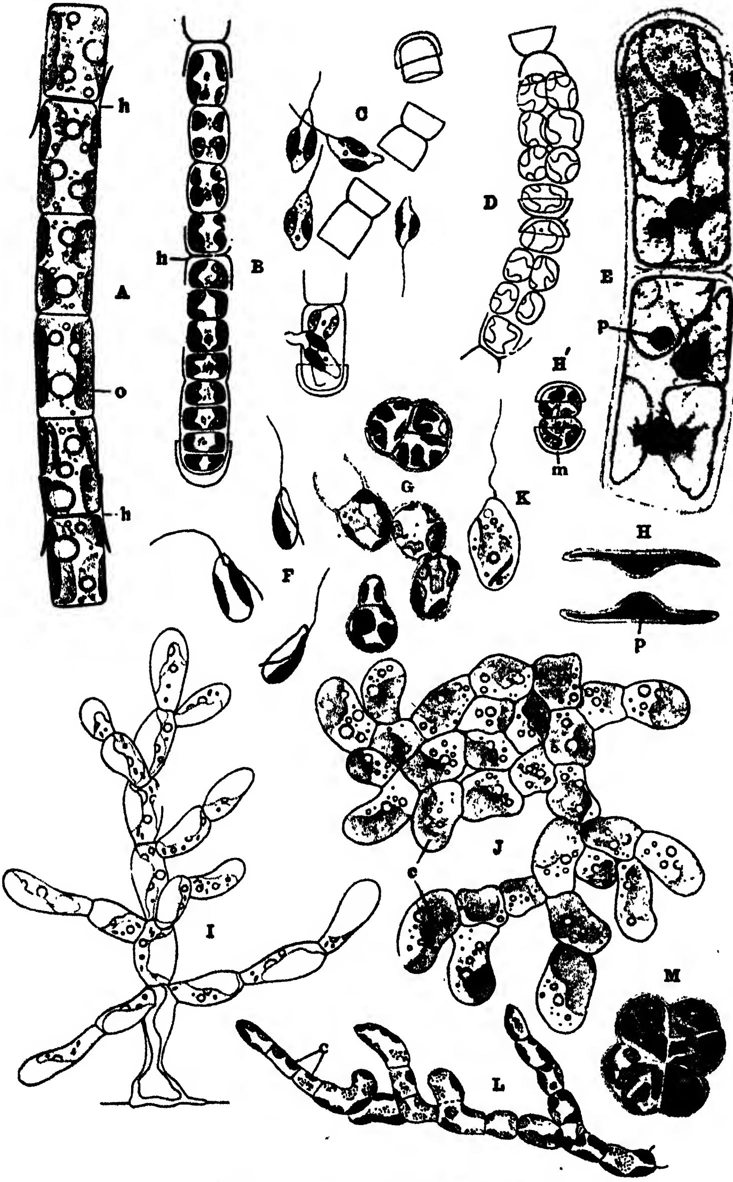

Fig. 163 [*for description see opposite*]

cultures, but Pascher records it from damp soil;[1] *Aeronemum* is an epiphyte on Bryophyta. *Monocilia* seems normally to occur as *Pleurococcus*-like packets of globose or ellipsoidal cells (fig. 163 G, M), although branched filaments of some length (fig. 163 L), as well as discoid filamentous expanses (fig. 163 J), are occasionally formed. It gives the impression of being a reduced form. The cells contain a number of parietal discoid chloroplasts or in other cases only a single large one (*M. simplex*, fig. 163 J), while the thin membrane as far as present knowledge goes is in one piece. The swarmers are typically Xanthophycean in *M. viridis* (fig. 163 F), although in *M. simplex* (fig. 163 K) only the long flagellum is present. They are produced in considerable numbers in the cells and in *M. viridis* two distinct sizes have been observed. Both aplanospores and akinetes are also known.

Aeronemum (92) typically forms small discs composed of radiating filaments, but the cells readily separate and lead an independent existence. The zoospores are stated to have but a single flagellum. There is practically nothing to differentiate the genus from *Monocilia*, with which it should probably be merged (cf. also (91 *a*) p. 160).

Heterodendron ((72) p. 356, (93)) closely resembles *Phaeothamnion* (p. 552) in habit. By contrast to the preceding genera it is an upright form attached by a specially differentiated basal cell (fig. 163 I). The swarmers are formed singly or after division and in one species akinetes are recorded.

Order IV. *HETEROSIPHONALES*

The common mud-alga *Botrydium* is now definitely established as the sole siphoneous representative of the Xanthophyceae at present known. *Botrydium granulatum* (38, 40, 42), which was long confused with *Protosiphon* (84), is found almost exclusively on drying mud, sometimes in countless numbers standing out in Mulberry-like masses. According to Kolkwitz ((43) p. 535) the vesicles are commonly encrusted with carbonate of lime. The individuals (fig. 164 A) are

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[1] Miss James has also found it in soil-cultures.

Fig. 163. A, *Bumilleria Klebsiana* Pascher. B–E, H, H′, *B. sicula* Borzi; B, thread with recently divided cells; C, liberation of swarmers; D, fragmentation accompanied by longitudinal division; E, two cells showing chloroplasts with pyrenoids (*p*); H, chloroplasts in optical section; H′, germinating cyst. F, G, L, M, *Monocilia viridis* Gern.; F, swarmers; G, M, cell-packets; L, branched thread. I, *Heterodendron squarrosum* Pascher. J, K, *Monocilia simplex* Pascher; K, swarmer. *c*, chloroplast; *h*, H-piece; *m*, membrane of cyst; *o*, oil; *p*, pyrenoid. (B–D after Borzi; E, H after Korschikoff; F, original drawing by Miss James; G, M after Chodat; L after Gerneck; the rest after Pascher.)

The ovoid zoospores (fig. 164 D) possess two (sometimes more) lateral chloroplasts and are devoid of a stigma, while the two flagella arise a little to one side of the apex ((43) p. 539, (54) p. 157); they are markedly metabolic, especially in the posterior region. The swarmers are set free by the gelatinisation of the apex of the vesicle (fig. 164 C). Aplanospores are formed when the plants are wet, but not submerged, i.e. in damp air. The young plants usually have at first a simple undivided rhizoid (fig. 164 E).

Miller ((54) p. 155) has described various methods of forming resting stages. In some cases the entire contents of a vesicle give rise to a single large cyst enveloped by a thick membrane, while in *B. Wallrothii* the contents divide to form a number of multinucleate cysts. In Miller's *B. pachydermum* the walls of the principal branches of the rhizoid-system undergo pronounced thickening so that the cavity may be altogether obliterated, while the large cyst formed in the vesicle is drawn into the substratum by contraction of the rhizoids. During periods of drought the protoplasmic contents migrate into the rhizoids and, in the case of *B. granulatum* (fig. 164 B), divide to form a large number of thick-walled globose or ellipsoid resting cysts which can either germinate directly or give rise to zoospores. In *B. tuberosum* the contents pass into the swollen ends of the rhizoids (fig. 164 J), each of which forms a cyst (39, 54). According to Miller (54) all types of cysts can germinate without a resting period.

Rosenberg (83) has recently reported the discovery of isogametes in *B. granulatum* which is monoecious, fusion of the gametes occurring even before they are liberated from the vesicle. The gametes are described as obpyriform, with the two flagella inserted at the broader end, and contain from one to three chloroplasts. The gametes meet and fuse by way of their posterior ends (fig. 164 K). The round zygote (fig. 164 M) germinates immediately. Parthenogenesis is also reported.

Printz ((81) p. 411) brings into relation with *Botrydium* a colourless coenocytic organism, *Geosiphon*, which lives in symbiosis with species of the blue-green alga *Nostoc* (104). This curious form has as yet only been found in autumn on clay soil, mainly on that of arable land, associated with *Anthoceros* and other Liverworts. The small colonies of the *Nostoc* are found in overground pear-shaped vesicles, a number of which arise from a branched weft of non-septate underground threads (fig. 165 A). The membrane is thick and stratified and consists of chitin, while abundant oil occurs in the contents. The only method of multiplication so far observed is by the formation of new vesicles, at first crowded with reserve-food, from the ends of the branches of the threads. *Geosiphon* thrives in inorganic nutritive solutions. According to Knapp (42 a) formation of vesicles on the threads depends on infection with *Nostoc*; he regards *Geosiphon* as a Phycomycete (cf. also (66 a)), the *Botrydium*-like vesicles being a result of the symbiotic union of the fungus with the alga.

AMOEBOID AND HETEROTROPHIC FORMS AMONG THE XANTHOPHYCEAE

Repeated reference has been made to the amoeboid state often assumed by the motile stages of the Xanthophyceae which may or may not be accompanied by loss of flagella. Permanently amoeboid types are, however, also known. Thus Pascher's ((63) p. 36, (72) p. 312) *Rhizochloris* (Heterochloridaceae) is a marine amoeba which contains several yellowish green chloroplasts (fig. 165 B, *c*) and apparently feeds largely by ingestion of solid particles; one species possesses a dark-coloured eye-spot. The same authority (69) has described an unnamed member of the Heterococcales (fig. 165 C) which reproduces by means of autospores, as well as by the liberation of amoebae (fig. 165 D) which possess one or more chloroplasts (fig. 165 E). These move with the aid of pseudopodia and exhibit ingestion of abundant organic particles, but after a varying interval round off, secrete a membrane, and constitute a new coccoid individual. In this form swarmers are apparently altogether suppressed and replaced by the amoeboid units. According to Pascher the distribution of the chloroplasts of the parent-cell among the two or four amoebae usually produced is not always an even one and he describes a case in which one amoeba received no plastids; the fate of this colourless form could not, however, be followed further.

In the case of *Perone* (71), with large cells inhabiting *Sphagnum*-leaves, swarmer-formation is rare, the reproductive cells usually assuming an amoeboid form and, on coming to rest, becoming completely rhizopodial before the coccoid stage is produced. Here too holozoic nutrition takes place abundantly. These observations show that the origin of amoeboid forms from algal types, which is very clearly evident in the Chrysophyceae and Dinophyceae, occurs also in the Xanthophyceae. *Rhizolekane* and *Stipitococcus* should also be recalled in this connection.

Myxochloris (68) is another amoeboid form with multinucleate naked protoplasts containing numerous chloroplasts and living in the water-storing cells of *Sphagnum*-leaves (fig. 165 I); more or less frequent contractile vacuoles (*v*) are discernible in the cytoplasm, while food is stored in the shape of leucosin and fat. Large multinucleate cysts (fig. 165 G, J) arise by the secretion of a thick membrane around the protoplast, and such cysts may either liberate their entire contents as a new amoeboid protoplast or by division of the latter produce uninucleate swarmers (fig. 165 N) or amoeboid units. These reproductive stages can form endogenous spores with the usual bipartite membrane. There is considerable analogy with *Myxochrysis* among Chrysophyceae (p. 536).

Myxochloris also shows much similarity to *Chlamydomyxa* which has

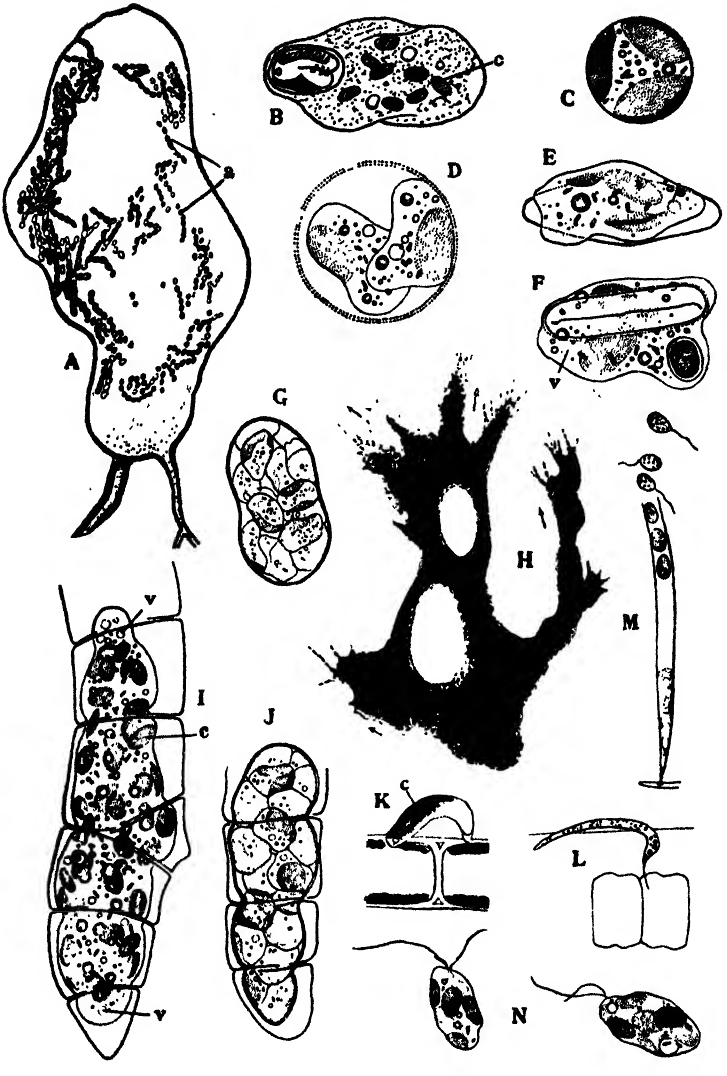

Fig. 165. Amoeboid and heterotrophic forms. A, *Geosiphon pyriforme* (Kütz.) Wettst. B, *Rhizochloris mirabilis* Pascher. C–F, Unnamed member of Heterococcales; C, coccoid cell; D, production of two amoebae; E, F, two amoebae engulfing a diatom. G, I, J, N, *Myxochloris sphagnicola* Pascher; G, J, swarmer-formation in cysts; I, plasmodium in water-storing cell of

been the subject of frequent investigation (cf. (a), (37), (75)) and is suspected of being a member of Xanthophyceae. *Chlamydomyxa*, however, as a general rule only forms its resting stages in the cells of the *Sphagnum*-leaves, whilst the large naked rhizopodial protoplasts (fig. 165 H) lead an independent existence.

A somewhat similar colonial organism has been described by Geitler (31) from marine cultures under the name of *Chlorachnion reptans*. The naked cells, which contain a number of green chloroplasts with a pyrenoid apposed to each, are united by numerous fine rhizopodia to form a flat network arising by repeated division of the cells. Nutrition is partly holozoic. Resting cysts are formed by withdrawal of the rhizopodia and rounding off of the protoplasts, followed by the secretion of a membrane. Whether this form belongs to the Xanthophyceae is still doubtful.

Contrary to the Chlorophyceae few independent colourless types are known among the Xanthophyceae. *Chloramoeba*, it will be remembered, can become colourless under certain circumstances. Lagerheim's *Harpochytrium* (3, 44 *a*, 47), an epiphyte on freshwater Algae and long suspected of being referable to this class, is now definitely established as belonging here by the discovery of a holophytic species (*H. viride*, fig. 165 K) by Scherffel ((86) p. 519). This genus belongs to the Chlorotheciaceae, the sickle-shaped cells which in most species lack chloroplasts being attached to the substratum by a basal stalk (fig. 165 L). In *H. viride* there is a single parietal yellow-green chloroplast. Multiplication is effected by zoospores, formed simultaneously in an elongate sporangium which becomes cut off from a basal vegetative portion by a septum (fig. 165 M). The ovoid swarmers have a single flagellum. Possibly the doubtful genus *Amoebidium* (93 *a*) also belongs here.

THE STATUS AND RELATIONSHIPS OF THE XANTHOPHYCEAE

As far as our present knowledge shows, the Xanthophyceae have not attained to as high a differentiation as the Chlorophyceae, the main development apparently centring about the palmelloid and coccoid types. It is noticeable, too, that at present few cases of sexual reproduction are reported and that these do not pass beyond the isogamous stage. This indicates a group that is possibly still in course

Sphagnum; N, swarmers. H, *Chlamydomyxa labyrinthuloides* Arch. K, *Harpochytrium viride* Scherff. L, *H. Hyalothecae* Lagerh. M, *H. Hedinii* Wille, liberation of swarmers. *a*, *Nostoc*-thread; *c*, chloroplast; *v*, contractile vacuole. (A after Wettstein; H after Hieronymus; K, L after Scherffel; M after Atkinson; the rest after Pascher.)

of evolution. By comparison with the Chrysophyceae, with which the Xanthophyceae share the paucity of highly evolved types and the absence of oogamous sexual reproduction, the flagellate phase is scantily represented. The majority of the Xanthophyceae appear to occur in freshwater, but *Halosphaera* and *Meringosphaera* (Heterococcales) are widely distributed in marine plankton and our knowledge of the simpler filamentous marine Algae is so imperfect that Xanthophyceae may yet be found among them.

The outstanding characteristics of the class are constituted by the special pigmentation of the chloroplasts, the absence of starch and the storage of oil, the prevalence of pectic compounds in the membranes, the distinctive flagellation and frequent amoeboid character of the swarmers, and the widespread occurrence of endogenous cysts with a membrane of two usually unequal pieces and commonly silicified (70). These features are clearly marked in many members of the class. Many of them are found also in the Chrysophyceae and are almost doubtless indicative of a relationship between the two classes (cf. p. 643). As Geitler (32) has pointed out, it is more the collective presence of the above characteristics that serves to distinguish the Xanthophyceae, since one or other of them is often ill developed in a given form or in certain habitats. He particularly draws attention to the fact that forms like *Tribonema* and *Chlorobotrys* are often found in nature with pure green chloroplasts, showing no preponderance of xanthophyll, and there is no denying that under certain conditions of the habitat the metabolism of Xanthophyceae and Chlorophyceae may come to be rather similar.[1] Geitler inclines to lay special stress on the features of the flagella which are very delicate and, even when of almost equal length, show differences in their movements, in the position in which they are held, and in their structure (99). One flagellum is beset with numerous fine cilia (fig 154 H, K), a type normal in the Chrysophyceae, although declared by Korschikoff (44) to be an artefact. Pascher emphasises the customary clear character of the cytoplasm and the frequent presence in the swarmers of small, highly refractive, crystalloidal or rod-shaped bodies of unknown nature; they seem to play a part in wall-formation. Steinecke (92 a) looks upon the Xanthophyceae as a reduction-series commencing with the filamentous forms which are supposed to be derived from Green Algae like *Microspora*. This view is, however, at present based on too slender a foundation to be seriously considered.

The affinities of Xanthophyceae with Chrysophyceae and Bacillariophyceae are considered on p. 642.

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[1] Dangeard (108) also describes a case of apparent change from the characteristics of Chlorophyceae to those of Xanthophyceae in *Scenedesmus acutus*.

The following is an epitome of the classification of Xanthophyceae adopted in the preceding matter:

I. *Heterochloridales:*
  (*a*) *Heterochlorineae:*
    1. *Heterochloridaceae:* Ankylonoton, Chloramoeba, Chlorochromonas, Chloromeson, Heterochloris, Nephrochloris, Phacomonas (?), Rhizochloris.
  (*b*) *Heterocapsineae:*
    2. *Heterocapsaceae:* Botryococcus (?), Chlorogloea, Chlorosaccus, Gloeochloris, Helminthogloea, Leuvenia, Pelagocystis (Clementsia).
  (*c*) *Heterodendrineae:*
    3. *Mischococcaceae:* Mischococcus.
  (*d*) *Heterorhizidineae:*
    4. *Heterorhizidaceae:* Rhizolekane, Stipitococcus.

II. *Heterococcales:*
    5. *Halosphaeraceae:* Acanthochloris, Arachnochloris, Botrydiopsis, Endochloridion, Halosphaera, Perone, Pleurochloris.
    6. *Myxochloridaceae:* Chlamydomyxa (?), Chlorachnion (?), Myxochloris.
    7. *Chlorobotrydaceae:* Centritractus, Chlorobotrys, Goniochloris, Meringosphaera, Monodus, Pseudotetraëdron, Tetraëdriella, Tetragoniella.
    8. *Chlorotheciaceae:* Characiopsis, Chlorothecium, Harpochytrium, Lutherella, Peroniella.
    9. *Ophiocytiaceae:* Ophiocytium.

III. *Heterotrichales:*
    10. *Tribonemaceae:* Bumilleria, Heterothrix, Neonema, Tribonema.
    11. *Heterocloniaceae:* Aeronemum (?), Heterodendron, Monocilia (Heterococcus).

IV. *Heterosiphonales:*
    12. *Botrydiaceae:* Botrydium, Geosiphon (?).

LITERATURE OF XANTHOPHYCEAE

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Class III. CHRYSOPHYCEAE

In the case of the Chlorophyceae and Xanthophyceae the majority of the species known at the present day are possessed of firm cell-walls in the ordinary vegetative condition and altogether show an "algal" construction. A considerable number of the forms belonging to the Chrysophyceae, however, possess naked protoplasts and are essentially "flagellate" in organisation. Until relatively recent times, in fact, the Chrysophyceae comprised only a wealth of flagellate types, the Chrysomonadineae, but thanks to the investigations of Pascher, Scherffel, Conrad and others it is now abundantly clear that these flagellate forms, just as in other classes, have advanced considerably in the direction of algal organisation. Moreover, the Chrysophyceae exhibit such a profound morphological parallelism with Chlorophyceae and Xanthophyceae that it is no longer warranted to regard them as something distinct from other groups of Algae, the more as the class is essentially holophytic and many of its members indeed wholly dependent on this method of nutrition. As in the Xanthophyceae sexual reproduction appears to be rare and never to be other than isogamous, an indication that, although highly evolved in some respects, the class has remained at a relatively low level in others. In one case (135) it has been shown that the individuals are haploid, and this is likely to be true of all the members of the class.

The Chrysophyceae appear in the main to favour relatively pure waters and seem often to occur in greatest abundance in cold winter weather (45) or in the cold streams and pools of mountainous tracts (30). Many occur in freshwater plankton, tending to attain a maximum in the layers beneath the surface of the water. In the sea they are abundantly represented by the Coccolithophoridaceae, although other families seem not to be as widely represented as in freshwater (7, 73, 128); Kolkwitz (58), however, records considerable numbers of naked Chrysomonadineae in Mediterranean plankton, and the Chrysophyceae may well be more abundant in the floating life of the sea than is at present apparent. Members of this class also appear to play a conspicuous part in the waters of certain kinds of salt-marshes (17). The bulk of the Chrysophyceae lose nearly all their distinctive characteristics in preserving media and often become so altered that recognition is impossible; attention should therefore be concentrated on the investigation of living material.

THE GENERAL CHARACTERISTICS OF THE CLASS

Like the Xanthophyceae the Chrysophyceae are characterised by the possession of chromatophores with a distinctive pigmentation, usually giving the individuals a golden-yellow or brown colour, although in waters rich in organic substance they often assume a green tint. The special coloration is in this case due to varying amounts of one or more accessory pigments (phycochrysin (33)) about which as yet little is known.[1] The chromatophores are parietal and usually few in number, often only one or two (cf. fig. 166 A, B); in the motile individuals they lie along the sides of the cell. In a number of cases (e.g. *Chromulina*, fig. 166 D; *Chrysamoeba*; *Hydrurus*, fig. 166 H; *Mallomonas pyriformis*, etc., cf. (18), (22), (26) p. 389, (29), (35)) they have been found to contain naked pyrenoid-like bodies, while in *Ochrosphaera* (135) the pyrenoids are attached by short stalks to the inner faces of the chromatophores (fig. 166 C, I).

True starch does not occur, although Pascher ((89) pp. 180, 194) records starch-like grains in a few cases. The products of photosynthesis are, however, mostly stored as oil and as whitish, highly refractive, usually rounded lumps of *leucosin* ((56) p. 401) (fig. 166 B, K, *l*) which constitute one of the marked characteristics of the class. In many cases the leucosin occurs as a prominent mass at the posterior end of the motile stages. The chemical composition of leucosin is unknown, although there is some probability that it is of the nature of a carbohydrate; it is readily soluble in most reagents and is not affected by iodine. According to Korschikoff ((61) p. 258) the leucosin-masses are vacuoles with very resistant walls enclosing a highly refractive substance. Contrary to most authorities he considers this to be of the nature of a protein, although no evidence for this view is given (cf. also (34) and p. 37). Apart from these inclusions, the protoplast of the Chrysophyceae, like that of the Xanthophyceae, is usually remarkably clear and free from granules. The cell-wall, when present, appears to consist largely of pectic substances (135).

All known Chrysophyceae are uninucleate. Relatively little information is available with reference to the structure of the nucleus, but it probably does not differ fundamentally from that of other Algae. In the resting condition the outer nucleus seems usually to show distinct chromatin granules (fig. 166 E), although Docquier (25) records it as structureless in *Anthophysa*.[2] There is a conspicuous caryosome (fig. 166 E, K). The chromosomes are generally rounded in form,

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[1] According to Gaidukov (33) the chromatophores of *Chromulina Rosanoffii* contain three pigments, viz. phycochrysin soluble in water and causing the golden coloration, and chrysochlorophyll and chrysoxanthophyll; the last two are soluble in alcohol and are believed to constitute modifications of the ordinary chlorophyll and xanthophyll.

[2] Not yet certainly established as a member of the class (cf. p. 540).

appearing as minute granules in *Monas* (81), while in *Rhizochrysis* (26) they are relatively large and often oval in shape (fig. 166 R). In *Ochromonas granularis* (27) they are stated to join to form a uniform ring at the equator of the intranuclear spindle, the ring splitting into two to supply the daughter-nuclei (fig. 167 O); a similar condition is reported in *Ochrosphaera* (135). According to Doflein the spindle in *Ochromonas granularis* arises from the caryosome and, if I understand him rightly, he believes the same to be the case in *Rhizochrysis*. In the latter there is a considerable lengthening of the spindle in the anaphase, while the poles broaden out and give rise to spherical bodies (fig. 166 S) which become enveloped by the rings of chromosomes, now losing their identity. The spherical poles of the spindle are believed to afford the daughter-caryosomes. Centrosomes have been recorded in a few cases (18) (fig. 168 O, P, *ce*).

Another very distinctive feature of the class is constituted by the cysts[1] which are gradually becoming known in more and more species. They are produced endogenously (fig. 166 J). In the preliminary stages of cyst-formation the protoplast usually becomes amoeboid, in the motile forms commonly losing the flagella (fig. 166 L, P). The cytoplasm acquires a foamy consistency and there is often an accumulation of oil and leucosin. Additional contractile vacuoles make their appearance (fig. 166 M), while a gelatinous envelope of varying width usually forms around the protoplast (cf. fig. 168 F). The latter then secretes near its periphery a hollow, spherical, cellulose membrane (fig. 166 L, *m*). After this the external cytoplasm accumulates towards one side where the membrane develops a papilla in which a definite opening subsequently appears as a result of solution of the primary membrane at this point (fig. 166 M). It is not altogether clear, however, whether this opening always arises secondarily. Subsequent to this the membrane thickens and becomes impregnated with silica, while the outer surface often develops elaborate sculpturing which is no doubt formed by the external cytoplasm (cf. figs. 168 G, 180 C). Part of the latter next usually passes through the pore into the interior of the developing cyst. Finally the aperture is closed from the inside by the production of a special plug, usually more or less conical in shape and as a general rule containing little or no silica (fig. 166 J, O, Q, *h*), while the remainder of the external cytoplasm gradually disintegrates.

According to Scherffel and Pascher ((110) p. 298, (122)) the cysts are often larger than the cells from which they are produced, which is in part due to increase in the volume of the cytoplasm, but is also ascribed to the cysts being of sexual origin. For the latter view, however, there is at present little evidence (cf. (29) p. 313) other than the observation that the young cysts sometimes contain two nuclei

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[1] See (29), (99), (110) p. 294, (122) p. 334, (123).

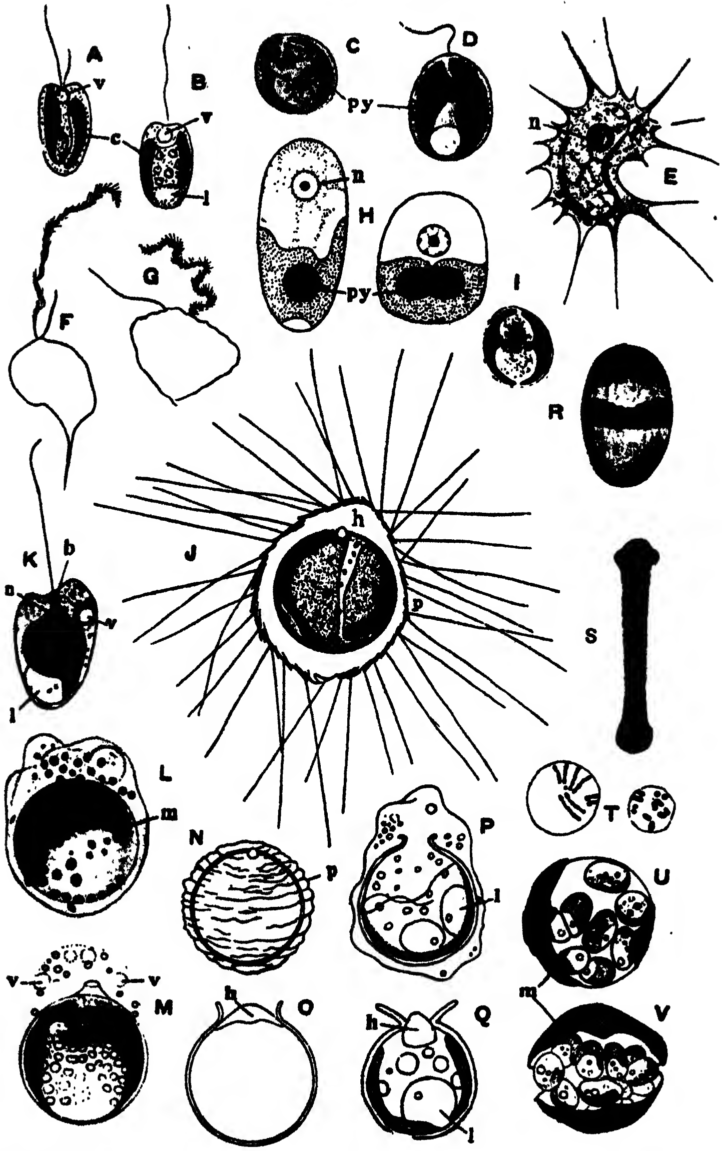

Fig. 166. General features of the Chrys A, *Ochrom* *abilis*
Klebs. B, *Chromulina ovalis* Klebs. C, I, *neapolitana* Schussen.,

which subsequently fuse (116). In germination the plug is dissolved and the contents of the cyst usually divide to form a number of motile cells which escape through the pore (fig. 178 O, P).

Pascher (99) draws attention to the fact that, when the periplast of the parent-individual is soft it is completely absorbed into the cyst, whilst when it is coarser it remains as an external envelope around the latter, either fitting closely (as in some species of *Chromulina*, fig. 166 N) or retaining more or less of its original shape so that the contained cyst is clearly distinguishable from it (*Mallomonas*, fig. 166 J; *Synura*).

The wall of the mature cyst always consists of two pieces which are mostly of very unequal size (fig. 166 Q), although in a few cases they are almost equal ((98) p. 243). In two palmelloid forms Pascher (107) records special thick-walled cysts, strongly encrusted with iron-deposits and composed of two equal or unequal pieces (fig. 166 U, V). Since the cysts of Chrysophyceae contain chromatophores and leucosin, they are readily identified as belonging to members of this class, quite apart from the characteristic structure of the membrane. Many such cysts are indeed known which have not yet been assigned to definite forms. They have also been found in diatomaceous earths (49) and other fossil deposits (24 *a*).

According to Petersen (112, 113) a further characteristic is to be found in the structure of the flagella. When two are present, one is beset along its whole length with fine cilia standing off at an acute angle,[1] while the second is of quite a different nature (fig. 166 F, G). When elongate (as in *Synura*, fig. 166 G), it consists of a thick basal part and a thinner whip-like extension, whilst when short it betrays no special structure. The ciliated flagellum shows undulatory move-

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[1] According to Korschikoff (59) this is an artefact. Even if this is true, it must imply a difference in structure between the flagella.

stalked pyrenoids. D, *Chromulina freiburgensis* Dofl., chromatophores with pyrenoids. E, *Rhizochrysis* sp., stained individual to show nuclear structure. F, *Uroglena Volvox* Ehrenb. and G, *Synura Uvella* Ehrenb., flagellar structure. H, *Hydrurus foetidus* (Vill.) Kirchn., chromatophores with pyrenoids. J, *Mallomonas mirabilis* Conrad, cyst within coarse envelope of parent. K, *Chromulina zartensis* Dofl., with two basal granules (*b*) below the flagellum. L, M, *Ochromonas*, two stages of cyst-formation; L, *O. perlata* Dofl., M, *O. crenata* Klebs. N, *Chromulina* sp., cyst enveloped by shrunken remains of periplast. O, cyst with a broad plug. P, Q, *Ochromonas* sp., two stages in cyst-formation. R, S, *Rhizochrysis* sp., two stages in nuclear division; R, commencing anaphase; S, telophase. T, *Ochrosphaera neapolitana*, meiosis in the zygote; on the left synapsis, on the right diakinesis. U, V, *Chalkopyxis tetrasporoides* Pascher, germinating cysts. *c*, chromatophore; *h*, plug of cyst; *l*, leucosin; *m*, membrane of cyst; *n*, nucleus; *p*, periplast; *py*, pyrenoid; *v*, contractile vacuole. (B after Klebs; C, I, T after Schwarz; D, E, K–M, R, S after Doflein; F, G after Petersen; H after Geitler; J after Conrad; the rest after Pascher.)

ments, whilst the other lashes like a whip. Petersen suggests that the former causes the forward movement, while the latter is responsible for the rotation of the individual. In diverse cases the flagella have been shown to arise from special basal granules (figs. 166 K, 167 N, O) which are connected to the nucleus or to a centrosome (fig. 168 O) by a rhizoplast.

The motile unicellular and colonial types are better represented in the Chrysophyceae than in any other group of the Algae and show even greater diversity than obtains among the Volvocales. In particular there is considerable variation in the number and length of the flagella, and this is seen also in the reproductive cells of the advanced sedentary types. In conformity with the grouping adopted in the preceding classes we may distinguish the three orders Chrysomonadales, Chrysosphaerales, and Chrysotrichales, including the motile forms and their immediate derivatives, the coccoid types, and the filamentous types respectively.

Order I. *CHRYSOMONADALES*

Here we have to distinguish the normally motile Chrysomonadineae, the rhizopodial Rhizochrysidineae, and the palmelloid Chrysocapsineae, each of which is best considered separately.

(*a*) THE MOTILE TYPE (CHRYSOMONADINEAE)

Among the Chrysomonadineae we can recognise four series of forms differing in their flagellation, although agreeing in many other respects. These are:

Chromulineae, with a single flagellum (fig. 167 A).
Isochrysideae, with two equal flagella (fig. 169 A).
Ochromonadeae, with two unequal flagella (fig. 167 L, M).
Prymnesieae, with one short and two long flagella (fig. 170).

The Unicellular Motile Forms

It is unnecessary to take these series separately, and the following account deals with the Chrysomonadineae as a whole. The unicellular *Chromulina*[1] is typical of the simpler Chromulineae (Chromulinaceae) and exhibits many of the characteristics of the class. The variously shaped cells (fig. 167 A–C) possess an apical flagellum which is often much longer than the body. The individuals are naked and in the majority of cases possess a soft periplast so that at times they

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[1] See (6*a*), (13), (17), (22), (29), (30*a*), (86), (91).

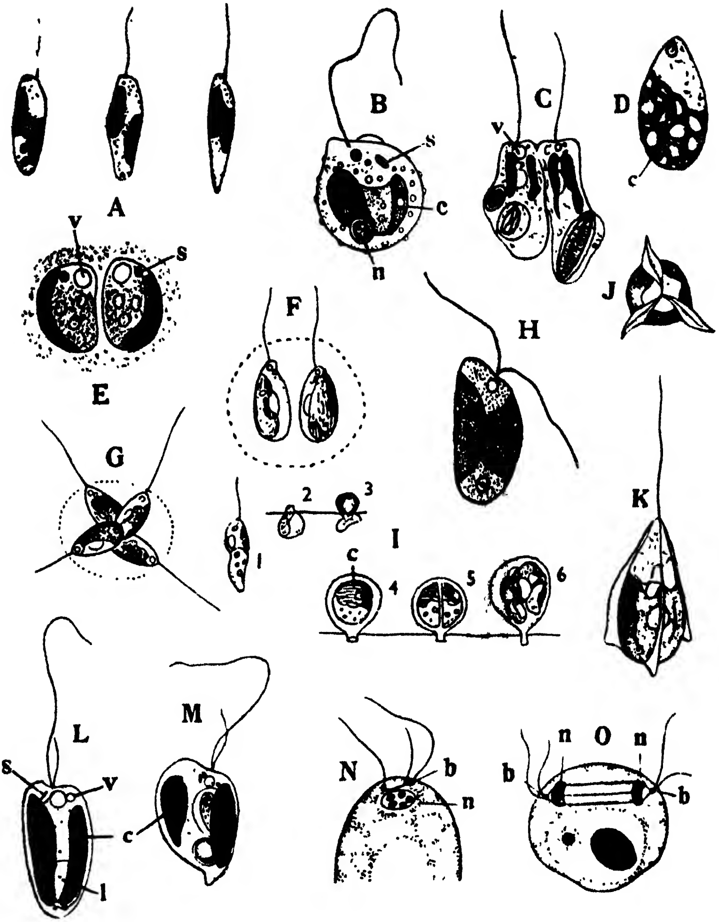

Fig. 167. A, *Chromulina nebulosa* Cienk., three individuals. B, *C. Pascheri* Hofeneder. C, *C. flavicans* Klebs, division, holozoic nutrition. D, *Chrysapsis fenestrata* Pascher. E, *Chromulina ovalis* Klebs, division. F, G, *C. Hokeana* Pascher, two- and four-celled colonies. H, *Wyssotzkia biciliata* (Wys.) Lemm. I, *C. Rosanoffii* (Woron.) Bütschli; *1*, vegetative individual; *2*, *3*, two stages in cyst-formation; *4*, mature cyst; *5*, *6*, germination. J, K, *Pyramidochrysis splendens* Pascher; J, view from the anterior end. L, M, *Ochromonas mutabilis* Klebs; M, individual showing metaboly. N, O, *O. granularis* Doflein, early and late stages in nuclear division. *b*, basal granules; *c*, chromatophore; *l*, leucosin; *n*, nucleus; *s*, stigma; *v*, contractile vacuole. (A after Scherffel; B after Hofeneder; E after Klebs; H after Cavers; I after Woronin; L, M after Conrad; N, O after Doflein; the rest after Pascher.)

exhibit abundant amoeboid change of shape (fig. 167 C); in some species, however, the periplast is firmer and then it commonly shows a verrucose surface (*C. verrucosa* Klebs, *C. Pascheri*, fig. 167 B), the warts being sometimes connected by a network of delicate ridges (*C. pyrum* Pascher).. As in other motile unicells one or two contractile vacuoles (*v*) are located at the front end and often there is a stigma (*s*). There are one or two (rarely more) large, well-defined, parietal chromatophores of a brownish colour, while a single mass of leucosin is usually lodged at the posterior end of the cell (fig. 166 B, *l*).

Multiplication is effected by longitudinal division ((56) p. 410), either of the motile individual (fig. 167 C) or more usually after the latter has come to rest and become enveloped by mucilage (fig. 167 E), and in some species (e.g. *C. Rosanoffii*) extensive palmelloid stages may thus arise. In *C. mucicola* Lauterborn (67) and *C. Pascheri* Hofeneder ((17) p. 172, (50)), numerous flagellated cells embedded in diffluent mucilage constitute the normal vegetative condition, swarming here only occurring in connection with reproduction (cf. *Chlamydomonas Kleinii*, p. 94). Such forms lead over to the Chrysocapsineae (p 541). In a few species (e.g. *C. Hokeana* Pascher (85)) there is a slight colonial tendency (fig. 167 F, G), the products of division remaining associated for a short time to form 2–8-celled motile colonies.

The distinctive cysts are known for a considerable number of species, and Conrad (22) has advocated a classification into distinct genera based on the surface ornamentation of their membranes. In *C. Rosanoffii* (*Chromophyton Rosanoffii* Woron. (147)), which not uncommonly occurs in aquaria, the cysts are formed in a very characteristic manner. The small individuals (fig. 167 I, *1*) come to rest at the water-level and a minute knob-like outgrowth is protruded (*2*) through the surface-film. This gradually enlarges (*3*) into a floating spherical cyst (*4*) containing almost the whole protoplasmic body, only a small stalk-like remnant remaining underneath. Since the concave chromatophore (*c*) reflects the light falling on the cysts, the latter when present in large numbers give a golden-brown sheen to the surface of the water (79). A similar phenomenon has recently been recorded for another species (44).

Other Chromulinaceae closely related to *Chromulina* are *Chrysapsis*[1] in which the chromatophore is very variable, sometimes reticulate and commonly not clearly differentiated (fig. 167 D), and *Pyramidochrysis* (84) in which the firm periplast is produced into three, slightly twisted, longitudinal ridges so that the cells appear triangular when seen from the end (fig. 167 J, K).

Not all the Chromulineae, however, possess the simple structure just described. In the genus *Microglena* (19, 86), for instance, the protoplast is provided with a firm envelope (fig. 168 A) in which,

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[1] See (16), (17), (86), (88), (130).

according to Conrad, one can distinguish a delicate inner smooth layer composed of cellulose (*i*) and an outer thicker layer of pectic substances (*m*), embedded in the surface of which are numerous minute lens-shaped masses of silica (*d*). In other words there is here a definite non-living cellular envelope (cf. however footnote 1 on p. 521), and this is probably true of all the Mallomonadaceae of which *Microglena* constitutes a relatively simple representative. A further indication of the higher differentiation of these forms is found in the complexity of the vacuolar apparatus. In *Microglena* (fig. 168 A, B) there is a large anterior non-contractile reservoir (*r*) opening to the exterior by a narrow canal at the apex of the cell, the firm membrane being interrupted at this point. Around this central reservoir are grouped a number (4–8) of much smaller contractile vacuoles (*v*) which communicate with the former by delicate canals. By their pulsation excreta are poured into the reservoir and from there pass to the exterior.

In the widely distributed plankton-genus *Mallomonas*,[1] in which the individuals are often of considerable size, numerous small imbricating circular or angular silicified scales (fig. 168 M) are deposited in the thin pectic envelope which is either hyaline or yellowish or brownish owing to impregnation with iron-salts. Some or all of the scales bear delicate hinged, likewise silicified needles ((117) p. 68) (fig. 168 I) which are sometimes hollow, are often of considerable length, and doubtless help to increase the floating capacity (fig. 168 H, L–N). In the closely allied genus *Pseudomallomonas* (9, 18) the needles are lacking and the base of the flagellum is surrounded by a definite collar, while in *Conradiella* ((17) p. 188, (20), (101) p. 566) the envelope takes the form of annular silicified plates (fig. 168 K) which are presumed to have arisen by the fusion of separate scales like those of *Mallomonas*. The cells of *Mallomonas* harbour a number of variously distributed contractile vacuoles, whilst in some species they are aggregated round a large anterior non-contractile reservoir (fig. 168 H, *r*), as in *Microglena*. There are one or commonly two lateral chromatophores (*c*), whilst the often large and conspicuous nucleus as a general rule occupies a central position (fig. 168 O, *n*). The flagellum is connected by a well-marked rhizoplast (*rh*) with a centrosome (*ce*) located near the nucleus (fig. 168 O).

Ochromonas (Ochromonadaceae),[2] among the Ochromonadeae, shows much the same level of differentiation and methods of reproduction as *Chromulina*, the chief difference being the presence of two flagella, one from four to six times the length of the other (fig. 167 L, M).[3] In many species the flagella arise from an emargination of

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[1] See (18), (51), (62), (86), (91).

[2] See (22), (27), (29), (86), (91).

[3] In *O. crenata* Klebs trichocysts, which are rare among Chrysophyceae, have been observed ((17) p. 215).

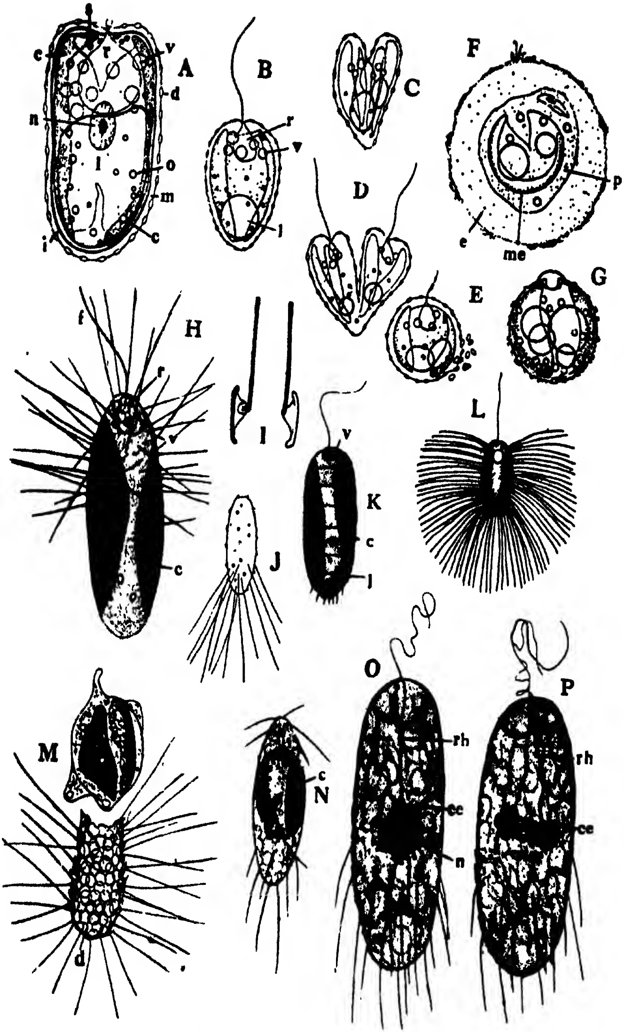

Fig. 168. Mallomonadaceae. A, *Microglena punctifera* Ehrenb., somewhat diagrammatic. B, E–G, *M. ovum* Conrad; E, F, stages in encystment; G, mature cyst. C, D, *M. cordiformis* Conrad, division. H, *Mallomonas helvetica* Pascher.[1] I, *M. elongata* Reverd., insertion of needles on scales.

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[1] The flagellum is actually nearly twice as long.

the front end which not uncommonly is more or less obliquely truncate, with a tendency for the dorsal edge to be specially protruded. The resemblance between several of the less specialised species of *Chromulina* and *Ochromonas* is so marked as to indicate that not too much stress should be laid on the number of flagella in this class. *O. sociata* Pascher (85), like *Chromulina Hokeana*, may temporarily form small colonies of 2–4 individuals embedded in mucilage.

Among the forms with two equal flagella (Isochrysideae) the simple unspecialised type comparable to *Chromulina* and *Ochromonas* is poorly represented, and none of the organisms that possibly belong here are well known. *Wyssotzkia* (fig. 167 H), originally described as a species of *Ochromonas* (148)[1] and regarded by some as a member of the Cryptophyceae, possesses cells with an obliquely truncated front end and two lateral chromatophores. According to Conrad (17) the individuals show marked metaboly and may become altogether amoeboid with loss of flagella; at such times holozoic nutrition may be observed. Reproduction takes place by division of non-motile cells in a palmelloid stage. Schiller's *Chrysidalis* (131) may be another simple member of this series.

Very widely distributed are the biflagellate Coccolithophoridaceae[2] which exhibit a more advanced construction, analogous to that of the Mallomonadaceae among Chromulineae. The bulk of the members of the former family are marine, occurring in large numbers in the sea all the world over, although probably most abundant in the Tropics. Latterly quite a number of freshwater forms have become known (12, 21, 124), whilst the genus *Hymenomonas*[3] described long ago by Stein is now recognised as belonging here. The individuals of *Hymenomonas* (fig. 169 A, B) possess a thick, though somewhat elastic envelope, consisting of an inner delicate membrane (*i*) of unknown composition and a thicker outer gelatinous portion (*g*). In the surface of the latter are deposited at fairly even intervals a large number of circular bodies (coccoliths) which consist of carbonate of lime (fig. 169 B, *c*). The vacuolar apparatus is anterior and similar to that

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[1] Cf. Lemmermann, *Forschungsber. Biol. Stat. Plön*, 7, 105, 1899.

[2] See (52), (54), (54*a*), (70), (72), (75), (115*a*) p. 63, (125), (127), (132).

[3] See (21), (53), (54*a*), (86).

J, *M. producta* (Zach.) Iwanoff. K, *Conradiella Pascheri* Conrad. L, *Mallomonas longiseta* Lemm. M, *M. mirabilis* Conrad, escape of amoeboid protoplast from envelope. N, *M. litomesa* Stokes, cyst-formation. O, P, *M. apochromatica* Conrad; O, cell-structure; P, division of nucleus and flagellum. *c*, chromatophore; *ce*, centrosome; *d*, silica scales; *e*, mucilage-envelope; *f*, flagellum; *i*, inner layer of wall; *l*, leucosin; *m*, outer layer of wall; *me*, membrane of cyst; *n*, nucleus; *o*, oil; *p*, protoplast; *r*, reservoir; *rh*, rhizoplast; *s*, stigma; *v*, contractile vacuole. (I after Reverdin; J after Smith; L after Lemmermann; the rest after Conrad.)

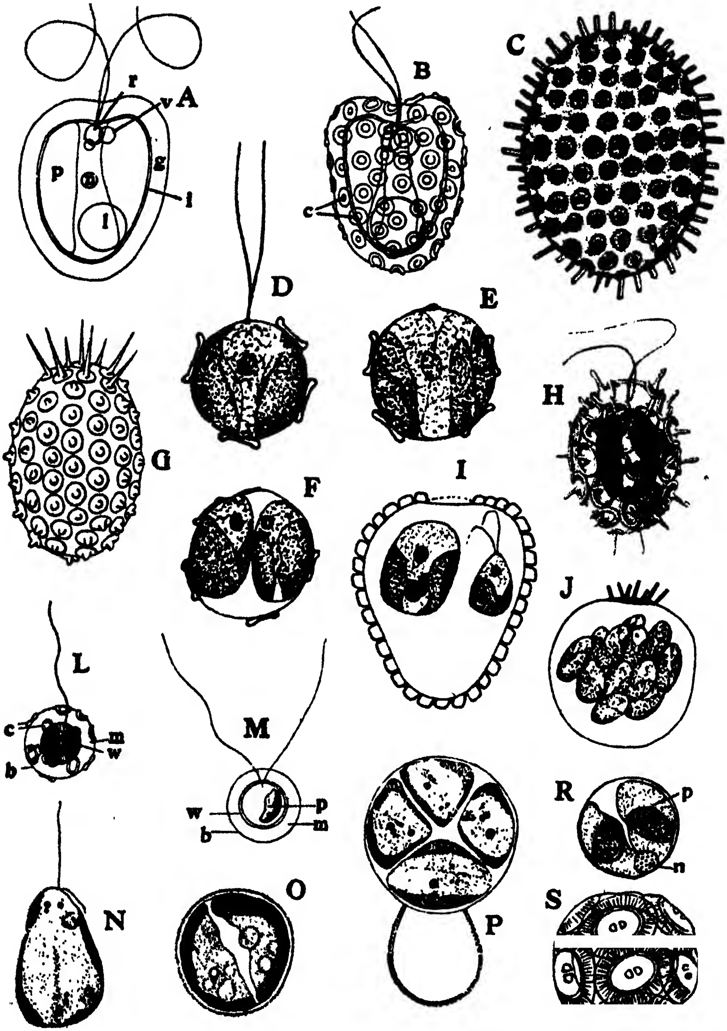

Fig. 169. Coccolithophoridaceae. A, B, *Hymenomonas roseola* Stein; A without and B with the coccoliths (*c*). C, *Pontosphaera nigra* Schill. D–F, L, *P. Huxleyi* Lohm.; E, F, stages in division of protoplast. G, *Acanthoica Schilleri* Conrad. H, *Syracosphaera subsalsa* (Conrad) Kamptner. I, *Calyptrosphaera oblonga* Lohm., division, the smaller protoplast a swarmer

of *Microglena* (fig. 169 A) and in other respects also the individuals recall the structure of the Chrysomonadineae already considered.

A considerable number of motile Coccolithophoridaceae are known, all with two equal flagella and chiefly differing among one another in the characters of the envelope. The latter varies greatly in thickness and is always gelatinous at first, although in many cases apparently undergoing calcification in later stages. The coccoliths are usually embedded in the surface of this envelope (fig. 169 B, D, L), to become rigidly united when the mucilage calcifies in the older individuals. In what Schiller (127) regards as the most advanced types (e.g. *Haplopappus*) the protoplast is enveloped in a thin homogeneous envelope of lime which he considers to be homologous with the entire group of coccoliths found in the less specialised species.

There are two principal types of coccoliths, those without and those with a central perforation. They are often produced into processes on the outer surface (fig. 169 C, H). Whilst in a considerable number of forms the coccoliths are of a uniform type, there are several species in which those at the anterior end (fig. 169 G) or in the median part of the body bear more or less marked spine-like processes which no doubt usually aid in flotation. Among the more remarkable forms are *Scyphosphaera* where the coccoliths over an annular zone are developed as large goblet-shaped structures with the opening facing outwards, and *Thorosphaera* (82) where they have the form of narrow projecting funnels. New coccoliths are successively formed internal to the old ones which gradually drop off. They are common objects in marine deposits past and present (74, 80*a*, 138) and are found ever since early Palaeozoic times (115). Certain of the marine genera (*Rhabdosphaera*, *Discosphaera*) are always devoid of flagella and should therefore really be included in the Chrysosphaerales (p. 548).

The Mallomonadaceae and Coccolithophoridaceae are parallel series with cells of similar structure, but differing in their flagellation and in the nature of the material secreted at the surface of their envelopes. Schussnig (134) has described a coccoid form (sometimes an epiphyte) under the name of *Ochrosphaera* (fig. 169 O) which likewise has an envelope harbouring carbonate of lime. This organism, however, reproduces by swarmers of the *Ochromonas*-type (fig. 169 N), so that

which will leave the envelope. J, M, *Syracosphaera mediterranea* Lohm.; J, formation of 16 swarmers (gametes?). N–P, *Ochrosphaera neapolitana* Schussnig; N, gamete; O, vegetative cell; P, vegetative propagation. R, S, *Coccolithus pelagicus* (Wall.) Schill.; R, protoplast; S, external view. *b*, surface layer of envelope; *c*, coccoliths; *i*, *w*, inner layer of wall; *l*, leucosin; *g*, *m*, mucilage-layer of wall; *n*, nucleus; *p*, chromatophore; *r*, reservoir; *v*, contractile vacuole. (A, B, G, H after Conrad; L, M after Lohmann; N, P after Schwarz; O after Schussnig; R, S after Lebour; the rest after Schiller.)

it appears that forms with a complex envelope have arisen in all three series of motile unicells.

Of the fourth series of Chrysomonadineae, *Prymnesium*(17, 76) is at present the only representative. The elongate ellipsoidal cells show a slight oblique truncation of the anterior end where the flagella arise (fig. 170 A). The short flagellum is straight and directed forwards and, according to Massart, serves solely for fixation (fig. 170 B, C), while the two longer ones are concerned in the movements. The latter consist of a series of forward and backward jerky progressions, often interrupted by periods of rest (cf. fig. 170 E). For the rest the cell-structure is like that of *Chromulina* or *Ochromonas*.

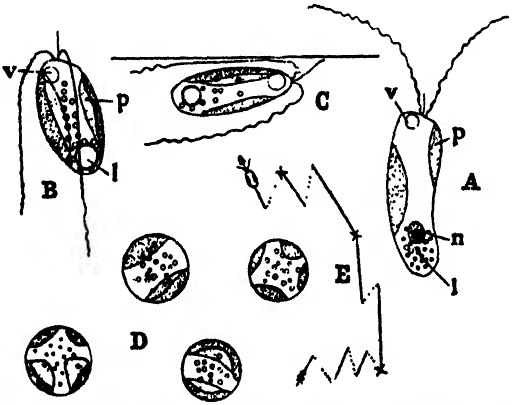

Fig. 170. *Prymnesium saltans* Massart (all after Massart from Conrad). A, cell swimming freely, side-view; B, cell attached to a solid body, front view; C, the same, side-view; D, palmelloid stage; E, path of an individual. *l*, leucosin; *n*, nucleus; *p*, chromatophore; *v*, contractile vacuole.

The ordinary motile unicell among Chrysomonadineae thus exhibits two stages of differentiation, both of which are not necessarily developed in all four series. We have on the one hand the naked type with a simple vacuolar apparatus (*Chromulina*, *Ochromonas*, *Wyssotzkia* (?), *Prymnesium*), on the other hand the type with a well-developed envelope and a complex vacuolar apparatus (Mallomonadaceae, Coccolithophoridaceae); according to Pascher ((89) p. 186) the forms belonging to the second type are also distinguished by possessing a more complex nuclear structure. It is essentially the simpler type of organisation that reappears in the numerous special developments exhibited by the Chrysomonadineae which will be briefly considered below (p. 523).

REPRODUCTION OF THE MOTILE UNICELLULAR FORMS

The reproduction of the simpler Chrysomonadineae has already been referred to in the preceding matter, taking place by longitudinal division of the motile or stationary individual, while the cysts constitute the resting condition. The reproduction of the more highly differentiated forms is imperfectly known, but shows certain special features. That of Mallomonadaceae probably customarily takes place by longitudinal division (fig. 168 D, P). In the case of *Microglena cordiformis* ((19) p. 428), where the individuals divide after losing their flagellum (fig. 168 C), each daughter appears to receive part of the envelope of the parent and to form a new envelope along the plane of division.[1] Whether this is generally true for the whole family is not known. Of special interest are those cases where the protoplast escapes from its envelope as an amoeba or as a *Chromulina*-like swarmer, as has been recorded by Conrad (15) in a species of *Mallomonas* (cf. fig. 168 M); in *M. akrokomos*, according to Schiller (130), this happens after division, one or both of the daughter-individuals leaving the parent-envelope. Cysts are commonly seen in Mallomonadaceae (cf. figs. 166 J, 168 E–G, N).

The reproduction of the Coccolithophoridaceae has been investigated by Schiller (127, 129) and Kamptner (54 a). In the freshwater forms *Hymenomonas* and *Pontosphaera*[2] *stagnicola* (12) direct division of the whole cell occurs, either in the motile condition or after withdrawal of the flagella. At an early stage both the envelope and the protoplast become constricted at the anterior and posterior ends, but it is only after the protoplast is completely divided into two halves that the constriction in the envelope gradually deepens and separates the two individuals. This is much as in *Microglena*, but does not appear to be the normal method in the marine forms, although the occurrence of short chains of 2–4 individuals in *Coccolithus* (*Coccolithophora*) is inexplicable except as a result of such division. Schiller, however, finds that as a general rule the protoplast, after withdrawal of the two flagella and after undergoing more or less marked contraction, either divides into two equal parts (fig. 169 E, F) which are liberated as naked swarmers through the widened flagellar aperture of the envelope; or, division is unequal (fig. 169 I), the larger protoplast remaining within the parent-envelope which it gradually fills, whilst the smaller escapes as a naked individual (cf. with *Mallomonas* above).

In addition Schiller observed a repeated division of the protoplast of certain individuals into as many as sixteen swarmers (fig. 169 J) which he regards as gametes, although fusion has not been seen

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[1] This behaviour of the envelope during division scarcely admits of interpreting it as a cell-wall.

[2] Kamptner (54) includes this genus in *Hymenomonas*.

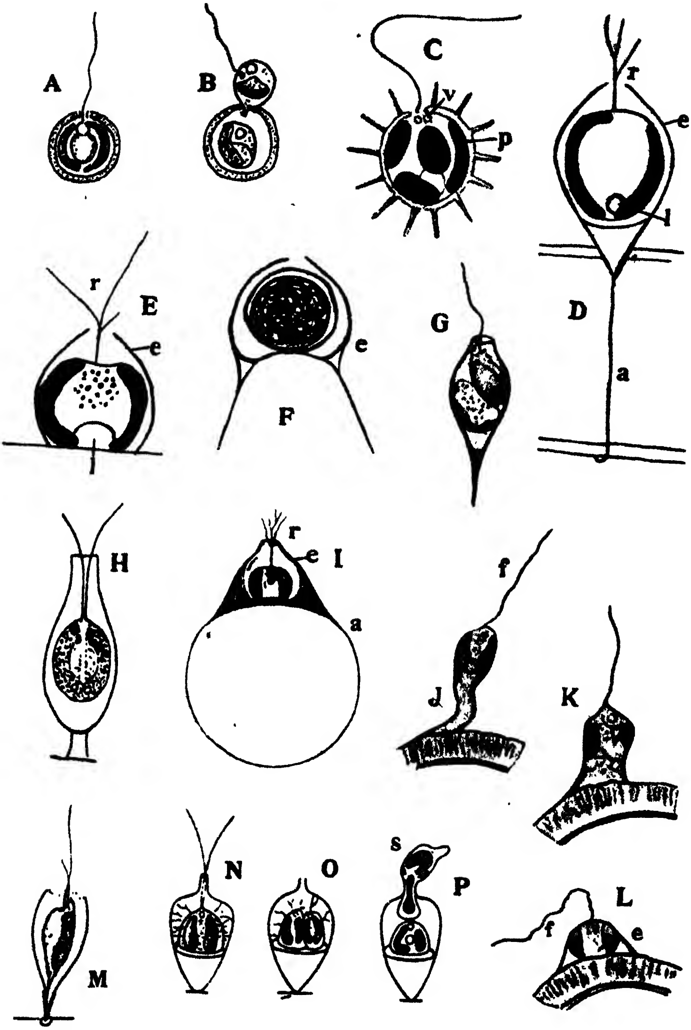

Fig. 171. The encapsuled Chrysomonadineae. A, B, *Chrysococcus rufescens* Klebs; B, reproduction. C, *C. dokidophorus* Pascher. D–F, *Chrysopyxis stenostoma* Lauterb.; D, side-view of individual on thread of *Mougeotia*, showing the annular mucilage-thread (*a*) and the apical rhizopodium (*r*); F, detached individual showing the saddle-like shape of the envelope (*e*). G, I–L, *C. Iwanoffii* Lauterb.; G, division, one half of protoplast about to

(cf. *Dinobryon*, p. 530). Cysts have not so far been found in the marine Coccolithophoridaceae, although Conrad ((17) p. 200) has recorded their formation in *Coccochrysis*. Schiller's ((132) p. 210) contention that the production of cysts is improbable appears unreasonable. Kamptner (54 *a*) suggests that the dormant stages are ordinary individuals devoid of flagella.

In the coccoid type *Ochrosphaera* Schwarz (135) records the formation of gametes, altogether resembling the zoospores except in the frequent presence of eye-spots. The same observer was able to establish the occurrence of reduction during the two nuclear divisions that follow almost immediately on sexual fusion and lead to the formation of four new individuals (cf. fig. 166 T, p. 510). This is the first fully authenticated case of sexual fusion with subsequent reduction in the Chrysophyceae. It should be noted that the zygote does not give rise to a cyst (cf. p. 509).

ENCAPSULED AND EPIPHYTIC TYPES

The encapsuled type (cf. p. 13) is well represented, although the majority of the forms involved are epiphytes. *Chrysococcus* (56, 86), however, has free-moving individuals with the structure of a *Chromulina*; the protoplast is enclosed within a spherical or ovoid, smooth (fig. 171 A) or diversely ornamented (fig. 171 C), rigid envelope separated from the protoplast by a slight space and possessing a narrow apical aperture for the protrusion of the often long flagellum; in several species the envelope is coloured brown by iron-salts and it is sometimes silicified ((17) p. 176). Multiplication is effected by longitudinal division of the protoplast, one daughter-individual adopting the envelope of the parent, whilst the other escapes and secretes a new one (fig. 171 B).

The epiphytic encapsuled type is met with in all series, except Prymnesieae, being represented by such widespread genera as *Chrysopyxis*[1] with a single flagellum (fig. 171 G), *Derepyxis*[2] with two equal flagella (fig. 171 H, N), and the species of *Dinobryon* of

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[1] See (32), (51), (69), (91), (111), (139).

[2] See (83), (86), (140), (142).

escape as a swarmer; I, complete individual with the attaching mucilage-ring (*a*); J, K, swarmer encircling the algal substratum; L, encirclement complete, flagellum still present, envelope forming. H, *Derepyxis amphora* Stokes. M, *Dinobryon* (*Epipyxis*) *marchicum* Lemm. N–P, *Derepyxis dispar* Lemm.; O, stage in division; P, escape of one (*s*) of the two protoplasts. *e*, envelope; *f*, flagellum; *l*, leucosin; *p*, chromatophore; *r*, rhizopodium; *v*, contractile vacuole. (A, B after Klebs; C after Conrad; D–F after Fritsch; G, I–L after Iwanoff; H after Stokes; M after Lemmermann; N–P after Pascher.)

the section *Epipyxis* (fig. 171 M) with two unequal flagella. In these the protoplasts do not usually fill the envelope and have a soft periplast admitting of a certain degree of metaboly as well as of holozoic nutrition. In *Derepyxis* there is often a septum across the lower part of the envelope, the protoplast then occupying the upper chamber; in this genus, too, the protoplast frequently appears suspended by a system of fine anastomosing lamellae whose nature is unknown (fig. 171 N, O). The envelopes are of very diverse shape and mostly possess a wide aperture through which the flagella project; the movements of the latter probably serve to waft food-particles towards the protoplast. Occasionally, however, the flagella are replaced by a branched rhizopodium (fig. 171 D, E, I, *r*) with the help of which small solid particles are ingested (69, 111). Pascher's *Lagynion* (90, 105) comprises a number of forms which appear permanently to have adopted this habit and in which flagellate stages are at present unknown.

The mode of attachment to the substratum (usually a filamentous alga) varies and is especially striking in *Chrysopyxis*, where the lower end of the envelope is saddle-shaped (fig. 171 F) and the corners are produced into a ring-shaped mucilage-thread which encircles the algal filaments upon which this epiphyte is found (cf. fig. 171 D, I). Direct motility in all these epiphytic types is only resorted to in connection with reproduction which is effected in the same way as in *Chrysococcus* (fig. 171 G, P), one half of the protoplast remaining within the parent-envelope, while the other escapes through the aperture as a naked swarmer. In *Chrysopyxis* (51) the swarmer becomes attached to the substratum by the posterior end, while retaining the flagellum (fig. 171 J, K); it then gradually passes round the algal filament, meanwhile secreting the encircling thread of mucilage, and it is only when it has returned to its starting-point that the production of the envelope commences (fig. 171 L). The formation of the envelope in *Dinobryon* is dealt with on p. 530.

COLONIAL FORMS[1]

Colonial Chrysomonadineae, several of which at times occur in great abundance, are known in all series except the Prymnesieae. They appear to be almost confined to freshwater. In most cases the colonies are more or less spherical, as in *Chrysosphaerella* (Mallomonadaceae, fig. 172 A), *Syncrypta* (Isochrysidaceae, fig. 172 B), *Synura* (fig. 172 F) and *Skadovskiella* (Synuraceae, fig. 172 E), and *Uroglena* (Ochromonadaceae); in *Chlorodesmus* (Synuraceae, fig

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[1] See also the "double" individuals described on p. 15.

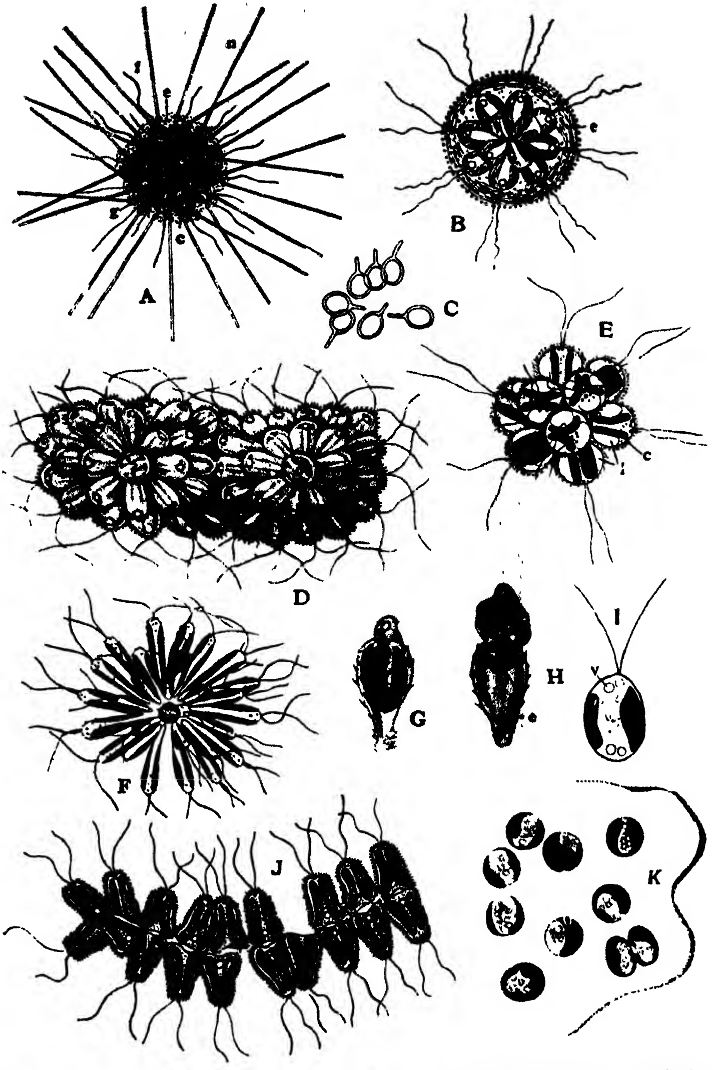

Fig. 172. Colonial Chrysomonadineae. A, *Chrysosphaerella longispina* Lauterb. B, *Syncrypta Volvox* Ehrenb. C, E, *Skadovskiella sphagnicola* Korschik.; C, siliceous rings from envelope. D, *Synura Uvella* Ehrenb., colony about to divide. F, *S. Adamsii* G. M. Smith. G–I, K, *S. Uvella*; G, H, escape of protoplast from envelope; I, swarmer; K, palmelloid stage. J, *Chlorodesmus hispidus* Philipps. *c*, chromatophore; *e*, envelope; *f*, flagellum; *g*, cup in which needle is inserted (in A); *l*, leucosin; *n*, needle; *v*, contractile vacuole. (A after Lauterborn; B, D after Stein; C, E after Korschikoff; F after Conrad; J after Philipps; the rest after Pascher.)

172 J), *Cyclonexis* (fig. 173 B), and *Chrysobotrys* (Ochromonadaceae, fig. 173 F), on the other hand, other forms of colonies occur. Among the Ochromonadeae colonies with a dendroid habit are common (cf. p. 529).

The only colonial form with uniflagellate individuals is Lauterborn's *Chrysosphaerella* ((66) p. 381), in which a number of cells are compactly grouped within a spherical mucilage-envelope (*e*) in which numerous small siliceous scales are embedded (fig. 172 A). The cells have a sharply differentiated envelope, two lateral chromatophores (*c*), and a number of vacuoles. At the front end of each individual the cellular envelope bears two little cups (*g*), disposed symmetrically on either side of the elongate flagellum (*f*). From the centre of each cup, and readily movable within it, there arises a single, long, hollow, siliceous needle (*n*), minutely bidentate at its apex. There are many points about this rare form that are still obscure.

More numerous colonial types are found among the Isochrysideae and in one of these, *Syncrypta* (86, 121, 139), the individuals exhibit the simple type of organisation which is poorly represented among the unicellular forms of this series. *S. Volvox* (fig. 172 B) is widespread in standing waters, though usually not abundant. As in *Chrysosphaerella* the obovoid cells are closely fitted together by their more pointed posterior ends, the whole group being surrounded by a wide mucilage-envelope (*e*) which appears granular owing to the presence of numerous minute rods of unknown nature. Bidder (3) records a doubtful species of this genus as an endophyte in sponges.

Among the Isochrysideae with more complex cell-structure, *Synura Uvella*[1] is a very widely distributed colonial form. The colonies, which are here usually devoid of enveloping mucilage, are composed of a very varied number of obovoid or ellipsoid cells, united by their more or less prolonged posterior ends (fig. 172 D). The cellular envelopes vary both in thickness and in ornamentation, being generally covered with short bristles, although sometimes verrucose or reticulate (4). According to Conrad ((17) p. 206) the envelopes are composed largely of pectic substances and are always more or less impregnated with silica (cf. also (112)). A second species, *S. Adamsii* (17, 137) (fig. 172 F), has narrower and more elongate cells, but otherwise shows similar characters.

In *Synura* the two chromatophores are parietal, but in Korschikoff's *Skadovskiella* (60) they are lodged in the middle of the cell owing to the presence of a large lump of leucosin between each and the surface of the protoplast (fig. 172 E). In this form, moreover, the periplast is covered with numerous siliceous bodies shaped like a screw-eye and forming a compact armour (fig. 172 C).

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[1] See (16), (22), (61), (86), (112), (139).

A somewhat different type of colony is seen in the rare *Chlorodesmus hispidus* (114) in which wedge-shaped cells, with a structure like that of *Synura*, are joined by their broader posterior ends to form band-shaped colonies in which the individuals are arranged in two rows (fig. 172 J). It is probable that the cells are connected by mucilage, since at certain times the colonies exhibit a rhythmic contraction and expansion, the contracted colony being only one-fifth the length of the expanded one. Conrad ((14), (16) p. 175) has described somewhat similar colonies in *Synura* (cf. also (146)).

The *Ochromonas*-type of individual has undergone a colonial development in several distinct directions. In *Uroglena*[1] (from which *Uroglenopsis* judging by Troitzkaja's investigations (143) cannot be distinguished) the cells are grouped at the periphery of a spherical or ellipsoidal mass of mucus. The individual cells are connected by a system of thread-like, forking mucilage-strands emanating from the centre of the colony (fig. 173 A); to these the cells (fig. 173 C) are attached by their pointed posterior ends. It appears that at times the mucilage-strands are not discernible. Büttner (7) has described a marine species of *Uroglena*.

Quite different are the colonies of *Cyclonexis* (141) (fig. 173 B) which consist of 10–20 narrow, wedge-shaped cells, bearing the two unequal flagella at the pointed anterior end and compactly arranged in one plane to form a circular plate with a small central space; the young colonies are somewhat funnel-shaped. Conrad's *Chrysobotrys* ((17) p. 216), again, has colonies resembling a loose *Spondylomorum* (fig. 173 F).

Compared with those of Chlamydomonadineae, the colonies of Chrysomonadineae show a less marked individuality. The movement is irregular, there being no definite anterior end, and the method of reproduction is altogether different, being effected by fission of the mature colonies (cf. figs. 172 D, 173 A) in those cases where it has been observed. Moreover, the number of individuals in the colonies is apparently always inconstant, since multiplication by longitudinal division of the cells may go on continuously, and no coenobial types have been evolved in this class. In *Synura* Pascher ((89) p. 156) records a propagation by naked swarmers (fig. 172 G, H) which escape from the bristly envelope; according to him these swarmers (fig. 172 I) exhibit a simplification of the vacuolar system. This return of the swarmers to a simpler type of organisation is a feature of some phylogenetic importance that appears to occur also in other highly organised Chrysomonadineae (cf. Coccolithophoridaceae, p. 521). In *Uroglena* Schiller (130) likewise describes a liberation of small spherical swarmers, subsequent to division of the mother-cell into four. Cysts

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[1] See (6*a*), (51), (80), (86), (117) p. 63, (130), (139), (149).

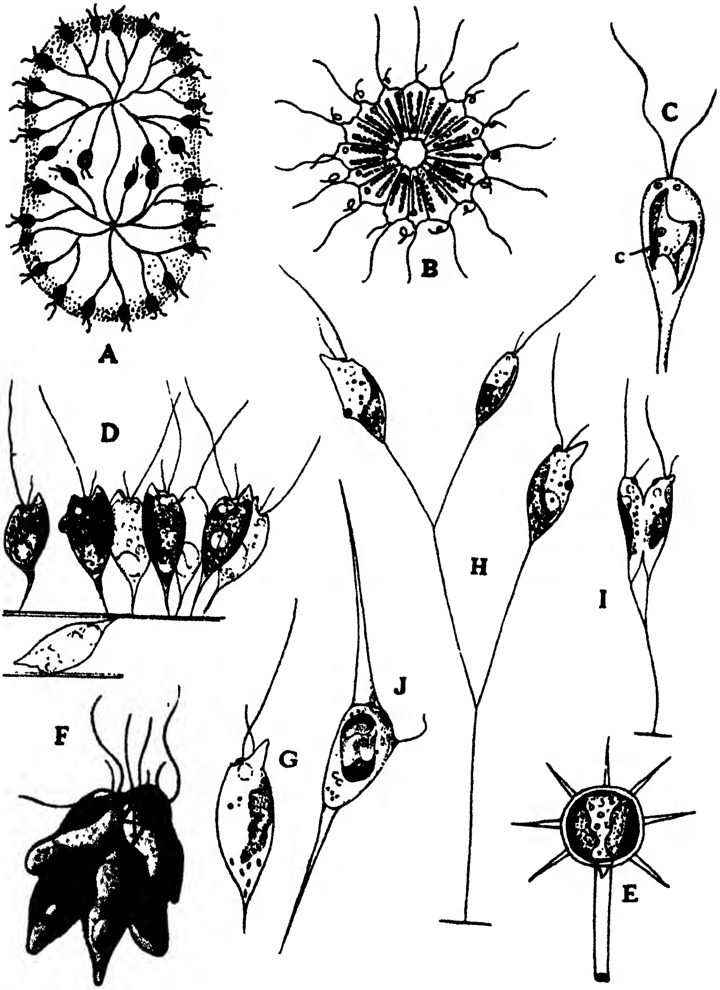

Fig. 173. Colonial Ochromonadeae. A, C, E, *Uroglena Volvox* Ehrenb.; A, colony about to divide; C, single individual; E, cyst. B, *Cyclonexis annularis* Stokes. D, *Ochromonas* sp., a number of individuals attached by the pseudopodial posterior end. F, *Chrysobotrys Spondylomorum* Conrad. G–I, *Chrysodendron ramosum* Pascher; G, detached individual; H, three-celled colony; I, division in a one-celled colony. J, *Diceras Chodati* Reverd. *c*, chromatophore. (A after Zacharias; C, E after Iwanoff; F after Conrad; J after Reverdin; the rest after Pascher.)

are known in *Synura* (11) and *Uroglena* (51) (fig. 173 E). Those of the latter have a long tubular process on one side.[1]

THE DENDROID TYPE OF COLONY

The dendroid type of colony is most markedly developed among Ochromonadeae, with Pascher's *Chrysodendron* (102) as the simplest representative. Several species of *Ochromonas* show a marked tendency to attach themselves by a pseudopodium-like prolongation of the posterior end to some substratum (fig. 173 D). This is a purely passing state and is not accompanied by loss of the flagella. *Chrysodendron* (fig. 173 H) is no doubt a further development of this tendency in which the flagellated cells are seated singly at the ends of a forked system of very delicate and elongate, colourless, elastic stalks. The individual cells (fig. 173 G) show the obliquely emarginate anterior end of an *Ochromonas* (p. 517), but this feature is emphasised by the prolongation of the dorsal margin on the side adjacent to the short flagellum. The posterior end of the protoplast is pointed and passes rather suddenly into the thin stalk. The individuals readily become detached from the latter and swarm away (fig. 173 G). The cells may multiply *in situ* by longitudinal division (fig. 173 I), after which each daughter-protoplast secretes a new stalk at its base, so that that of the parent appears to have forked into two.

The genus *Dinobryon*[2] includes a large number of non-colonial types, some of which are epiphytes (cf. p. 523) whilst others are freely motile.[3] A certain number, however, form dendroid colonies (fig. 174 B, G) which are abundant constituents of freshwater plankton, while a few species (e.g. *D. balticum* (Schütt) Lemm.) are found in coastal waters; most, if not all, of these are probably freshwater forms that can survive in the marine environment ((128) p. 61). In all cases, whether unicellular or colonial, the individuals are enclosed within a wide campanulate or cylindrical envelope, more or less pointed at the base and with a wide anterior aperture (fig. 174 A); the envelope is not uncommonly coloured yellow or brown by oxide of iron. The individual protoplasts are usually markedly metabolic and strongly resemble an *Ochromonas* (fig. 174 A). They are drawn out at the posterior end

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[1] The cysts described by Moore (80) can hardly be normal, as they are quite unlike those of other Chrysophyceae. Possibly they are stages of a parasite.

[2] See (56), (62), (91), (136), (139).

[3] A remarkable planktonic form that belongs to this affinity is Reverdin's *Diceras* ((117) p. 50), so far only known from the Lake of Geneva. The individual is lodged in an ovoid envelope with a small lateral orifice through which the two flagella at times project (fig. 173 J). The envelope is produced at either end into long pointed processes, one of which stands at an angle to the other.

into a short contractile thread (*t*) which is attached a little to one side of the base of the envelope. By means of this thread the cells are not only able to withdraw somewhat into the envelope, but can also travel along its side until they reach the aperture (fig. 174 J). The hyaline apex of the protoplast is, as in *Chrysodendron*, especially amoeboid and hollowed out to form a kind of cytostome through which solid particles can be ingested.

Multiplication is effected as usual by longitudinal division, one daughter-individual (sometimes smaller than the other, (129) p. 336) in the non-colonial types escaping as an *Ochromonas*-like swarmer which sooner or later forms a new envelope (cf. *Chrysopyxis*, etc.). In the colonial types one or both daughter-individuals effect a lodgement at the inner edge[1] of the rim of the parent-envelope (fig. 174 J) and there secrete a new one (fig. 174 L, M). In this way variously branched aggregates are produced (fig. 174 B, G). The protoplasts may also occasionally escape as swarmers without previous division.

In the formation of the envelope ((56) p. 399, (62) p. 301) a small funnel-shaped piece first arises at the base and thereupon the protoplast rotates on its axis, following a spiral course, and slowly secretes the remainder of the envelope. When the latter is complete the protoplast withdraws to the base. According to Pascher (98) the envelope is composed of successive thimble-shaped segments which are fitted into one another and are clearly recognisable in certain species (e.g. *D. Utriculus*) after boiling with potash and staining with Congo red (cf. fig. 174 F). In the closely allied epiphyte *Hyalobryon*,[2] one of whose species forms similar dendroid colonies, the projecting ends of these segments are visible without further treatment (fig. 174 C, H, I, N). According to Pascher a similar structure of the envelope is recognisable in *Chrysopyxis* and will probably be found in the envelopes of all the encapsuled Chrysomonadales.

Schiller (129) has reported the fusion of swarmers (isogametes) produced by longitudinal division and liberation of the protoplasts of *Dinobryon Sertularia* (fig. 174 O–R). The zygotes soon lose their flagella and sink to the bottom. This is so far the only record of sexual reproduction among motile Chrysophyceae. In many species of *Dinobryon* the cysts are formed just outside the aperture of the envelope within a special spherical membrane (fig. 174 D, E). The cysts are provided with a short projecting process, not so marked as in the case of *Uroglena*.

Dendroid colonies are also found among the Chromulineae in

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[1] On the outer edge in *D. coalescens* (cf. (128) p. 61), as well as in *Hyalobryon ramosum*. Gessner (43 *a*) regards this as an earlier step in colony-formation among these forms than the cases in which the daughter-individuals are attached within the parent-envelope.

[2] See (43), (66), (86), (111).

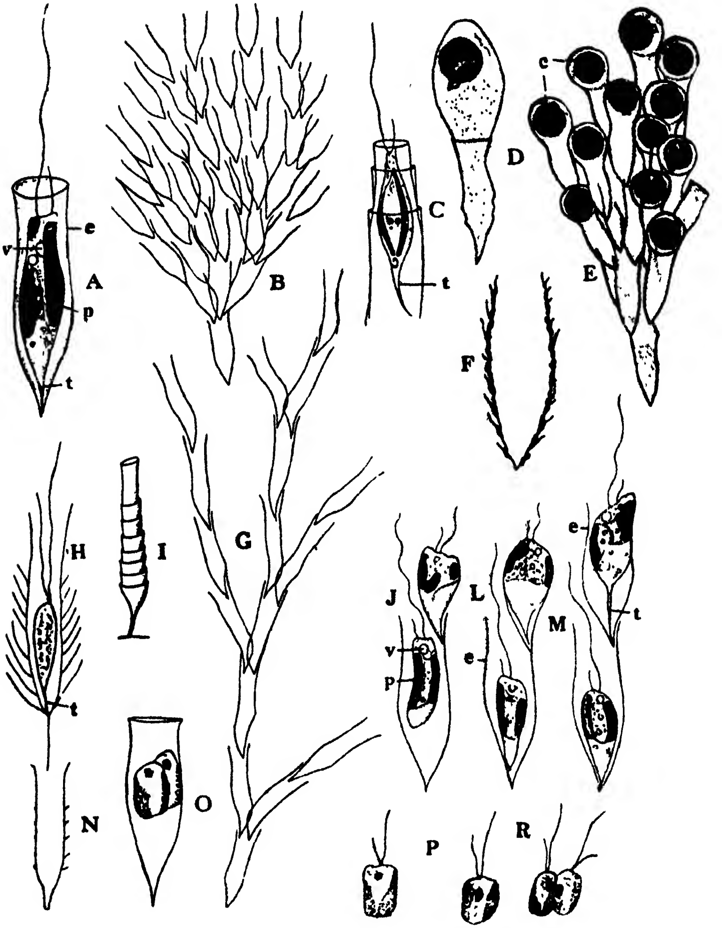

Fig. 174. *Dinobryon* and *Hyalobryon*. A, B, E, J–M, O–R, *Dinobryon Sertularia* Ehrenb.; A, single cell; B, colony; E, colony with encysted individuals; J–M, formation of new envelope after division; O, envelope with two swarmers; P, swarmers (gametes); R, fusion of same. C, *Hyalobryon ramosum* Lauterb., single cell. D, *Dinobryon cylindricum* Imhof var. ***divergens*** Lemm., encysted individual. F, *D. Utriculus* Stein, disorganising envelope. G, *D. cylindricum* var. ***palustre*** Lemm., colony. H, N, *Hyalobryon mucicola* (Lemm.) Pascher; N, envelope. I, *H. Voigtii* Lemm., envelope. *c*, cysts; *e*, envelope; *p*, chromatophore; *t*, contractile thread; *v*, contractile vacuole. (A, J–M after Klebs; B, G, I after Lemmermann; C after Lauterborn; D, E after West; F after Pascher; H after Bachmann; N after Smith; O–R after Schiller.)

Pedinella hexacostata Wyssotzki ((17) p. 180, (148)), belonging to the family Cyrtophoraceae. This family comprises a number of highly specialised epiphytes, the majority of which are attached to the substratum by contractile stalks (cf. fig. 175 E). The cells of *Pedinella* are ovoid and are provided with six slight longitudinal prominences which are occupied by as many parietal chromatophores (fig. 175 A, C). The anterior end, as in all Cyrtophoraceae, is highly metabolic and bears the long flagellum (*f*) centrally, while the margin is produced into a ring of short tooth-like rhizopodia (axopodia) by means of which holozoic nutrition is carried on. In *Cyrtophora* (87), in which the formation of colonies is not yet recorded, the rhizopodia are much longer than the flagellum (fig. 175 G), whilst in the third genus *Palatinella* (68) the latter is exceptionally short.

The rhizopodia in these forms are composed of an axial rod surrounded by a thin layer of streaming cytoplasm (fig. 175 D) and can under certain circumstances be withdrawn. According to Pascher ((97) p. 16) small particles are not only taken up by the peripheral cytoplasm of these structures, but collectively they may act as a trap for larger particles; when such are retained, the rhizopodia are stated to curve inwards and to thrust the object among the pseudopodia formed by the anterior extremity of the protoplast (fig. 175 F).

The individuals of *Pedinella* are attached by elongate delicate stalks, apparently similar to those of *Chrysodendron*; if the cells divide *in situ*, each daughter-protoplast secretes a new stalk (fig. 175 B), so that a forked colony originates. Conrad (17) describes how reproduction is effected by detachment of the cells which in some cases carry with them part of the underlying stalk attached to their posterior end.

The dendroid habit among Chrysomonadales is not as specialised a condition as in the Volvocales, and for that reason has not been considered as a separate series. In all cases the individuals are provided with their full motile equipment, and in the *Dinobryons* the whole colony is in fact free-swimming. But even in sedentary types, like *Chrysodendron* and *Pedinella*, resort to the motile stage merely requires detachment of the cell. These features are in conformity with the dominance of the flagellate habit among the Chrysophyceae.

(*b*) THE RHIZOPODIAL AND AMOEBOID TYPES (RHIZOCHRYSIDINEAE)

While the genera above discussed are all holophytic, holozoic nutrition is more or less frequently resorted to by many of them. Especially forms like *Chromulina*, *Ochromonas*, and *Chrysodendron*, with a soft periplast admitting of a ready protrusion of pseudopodia, have frequently been recorded as enveloping small food-particles within nutritive vacuoles from which the remnants are excreted after digestion (102, 121). A certain number of forms that are more highly equipped in this respect have already been noticed, viz. the species of *Chrysopyxis* (p. 524), in the sedentary individuals of which the flagellum is replaced by a branched rhizopodium (fig. 171 D, E); *Lagynion* (p. 524) where this condition is permanent; and the

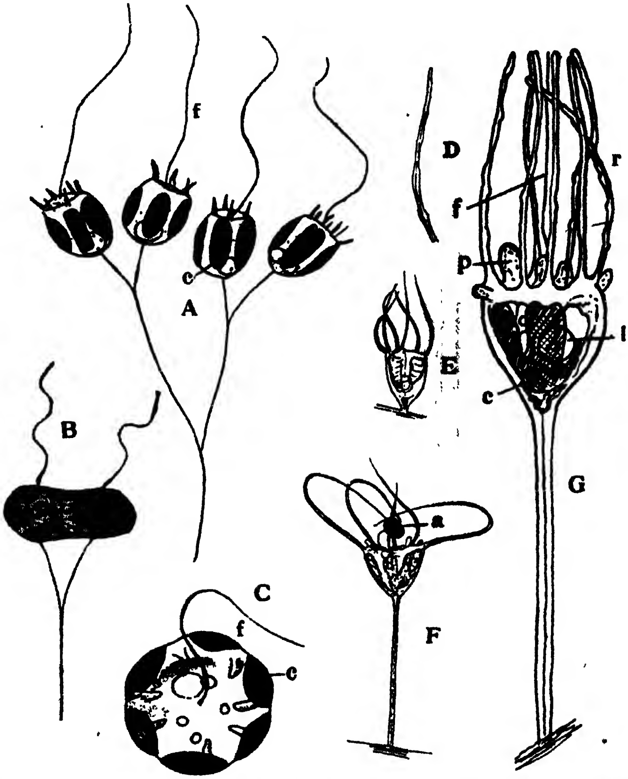

Fig. 175. The Cyrtophoraceae. A–C, *Pedinella hexacostata* Wyssotz.; A, colony; B, dividing individual; C, individual viewed from anterior end. D–G, *Cyrtophora pedicellata* Pascher; D, part of a rhizopodium; E, individual with contracted stalk; F, cell enveloping a cryptomonad (*a*) with its rhizopodia; G, mature individual. *c*, chromatophore; *f*, flagellum; *l*, leucosin; *p*, pseudopodium; *r*, rhizopodium. (A, C after Conrad; B after Wyssotzki; the rest after Pascher.)

Cyrtophoraceae, with their characteristic rhizopodia, among whom a reduction of the flagellum is plainly evident.

In the same way *Chrysamoeba radians* Klebs[1] may at one time appear as an ordinary *Chromulina*-individual (fig. 176 A), at other times assume a completely rhizopodial habit (fig. 176 B) with loss of flagella (cf. *Heterochloris*, p. 471). Pascher ((97) p. 19) has described a similar case in a species of *Ochromonas* (cf. also his *Brehmiella* (103)). The same authority ((89) p. 158) has, moreover, shown that the swarmers of *Synura* may become amoeboid or may even be liberated as amoebae from the very first; such amoebae, further, in many cases subsequently develop into rhizopodial stages (fig. 176 C). Conrad (15) has similarly described the escape of amoeboid stages in *Mallomonas* (cf. p. 521 and fig. 168 M), whilst Haye (48) has recorded them in *Dinobryon divergens* (cf. also (97) p. 13). The assumption of the amoeboid or rhizopodial habits does not necessarily involve the adoption or the increased adoption of the holozoic method of nutrition, but in most cases no doubt the two go hand in hand.

A considerable number of rhizopodial forms have, however, become known which are proved to belong to the Chrysophyceae by the nature of their cell-contents, but appear to have lost the capacity of forming swarmers; they cannot therefore be referred definitely to any one of the series of the Chrysomonadineae. These are the forms grouped by Pascher (91) as Rhizochrysidineae. A simple example of this type, showing many analogies with *Chrysamoeba* in its rhizopodial stages, is *Rhizochrysis* (26, 91), first described by Scherffel (120) as a *Chrysamoeba*. Here the individuals commonly occur in small aggregates and bear delicate, sometimes branched rhizopodia, but otherwise show all the typical characteristics of Chrysophyceae (fig. 176 D). *R. crassipes* Pascher has broad pseudopodia (fig. 176 G).

Geitler ((40) p. 631) has described a marine rhizopodial organism *Platychrysis*, in which two flagella are always present, although apparently not normally functional. The cells of this organism (fig. 176 I) are flattened with a concave under-surface from the middle of which the flagella arise; the latter are usually rolled up like a watch-spring (see the right-hand cell in fig. 176 I).

In Lauterborn s *Chrysidiastrum* (55, 91) approximately spherical individuals with delicate radiating rhizopodia are united by coarse protoplasmic strands to form short chains (fig. 176 F), while *Chrysarachnion* (95) consists of a one-layered network of more or less numerous (up to 200) individuals connected by delicate rhizopodia (fig. 176 E), which in this case are practically confined to the plane of the net (cf. *Chlorachnion*, p. 501). The nets can act like a cobweb and entrap unicellular organisms of moderate dimensions, and

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[1] See (28), (56) p. 406, (111); cf. also (117) p. 73.

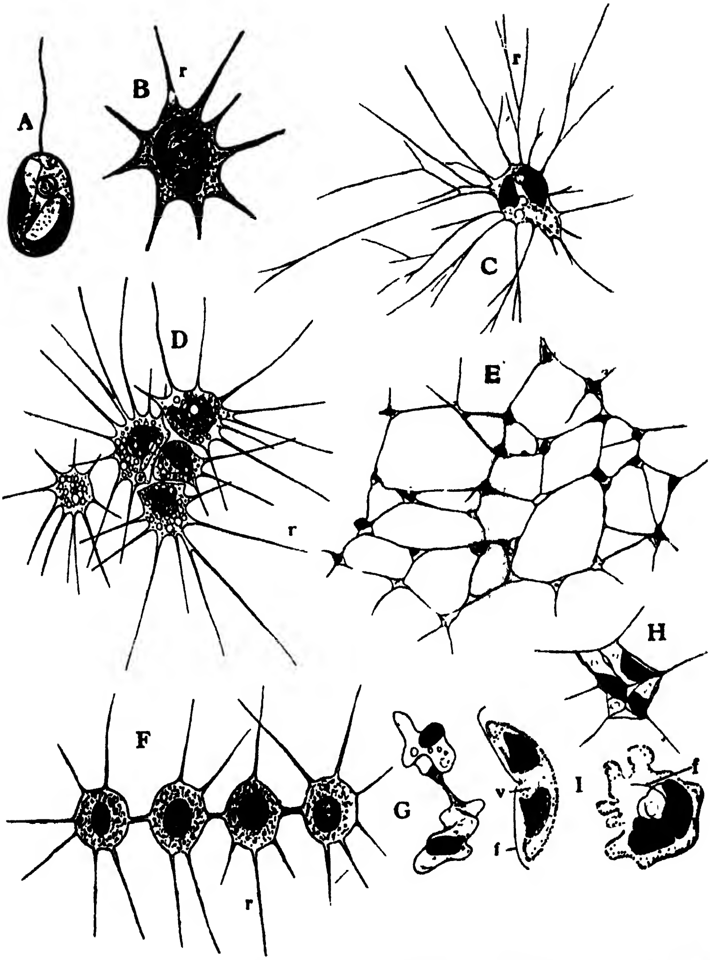

Fig. 176. Rhizochrysidineae. A, B, *Chrysamoeba radians* Klebs; A, flagellate and B, rhizopodial stages. C, *Synura Uvella* Ehrenb., rhizopodial stage of swarmer. D, *Rhizochrysis Scherffelii* Pascher, the left-hand individual without a chromatophore. E, H, *Chrysarachnion insidians* Pascher; E, part of a large net; H, division into three. F, *Chrysidiastrum catenatum* Lauterb. G, *Rhizochrysis crassipes* Pascher. I, *Platychrysis pigra* Geitl.; on the left, side-; on the right, surface-views of an amoeboid individual. *f*, flagellum; *r*, rhizopodia; *v*, contractile vacuole. (A, B after Klebs; D after Scherffel; F after Lauterborn from Pascher; I after Geitler; the rest after Pascher.)

Pascher describes how such foreign bodies become gradually enclosed in a weft of rhizopodia produced not only from the individuals in the immediate vicinity, but even from those which are not in direct contact with the body.

Pascher (93) has made us acquainted with a number of striking epiphytes belonging to this series. *Lagynion* (p. 524) should of course be included here. *Chrysocrinus* has a typical Chrysophycean protoplast encased within a firm and thick envelope which has the shape of a depressed hemisphere and is attached by its flat surface to freshwater filamentous Algae (fig. 177 M, N). The envelope (*e*) is impregnated with carbonate of lime and in older individuals is coloured yellow-brown by iron-salts. It is pierced by numerous fine pores (*o*) through which delicate rhizopodia (*r*), in part of considerable length and often branched, project radially (fig. 177 N); these serve to absorb Bacteria and other small organic particles. Multiplication is effected by division of the protoplast into two or four parts, prior to which the rhizopodia are often drawn in; the daughter-protoplasts escape through the pores and crawl about as amoebae from which no doubt the mature individuals are again produced.

Rhizaster (93) shows resemblances to the Cyrtophoraceae (p. 532). The individuals are contained within a close-fitting goblet-shaped cellulose envelope with a wide aperture and borne at the end of a long stalk (fig. 177 A). The protoplast is produced into a number of long horizontally extended rhizopodia (*r*), which are grouped around the amoeboid front end (fig. 177 B). Reproduction is effected as in other encapsuled types, one half protoplast remaining within the envelope, whilst the other crawls as an amoeba down the outer surface of the envelope and the stalk (fig. 177 D, E) till it reaches the substratum. This organism has also been observed to form typical cysts, produced as in *Dinobryon* in a special vesicle outside the aperture of the envelope (fig. 177 C).

The cohesion of the individuals in *Chrysidiastrum* and *Chrysarachnion* may perhaps be regarded as a preliminary step towards the completely plasmodial condition realised in Pascher's *Myxochrysis* (96). In the normal condition this organism occurs as a multinucleate plasmodium (fig. 177 F, G) surrounded by a coarse envelope (*e*), coloured brown by ferric hydroxide. Within the protoplasm there are usually numerous small plate-shaped chromatophores (*c*), although some plasmodia are colourless; there are numerous contractile vacuoles (*v*), oil-drops, and leucosin-masses (*l*). Movement is effected by blunt pseudopodia and the organism exhibits both holophytic and holozoic nutrition. Fusion of plasmodia commonly occurs. At times the protoplasm becomes cleft into numerous portions which are uni- or multinucleate and with or without chromatophores. These subsequently encyst and develop a thick membrane (fig. 177 L). From these cysts there arise, with or

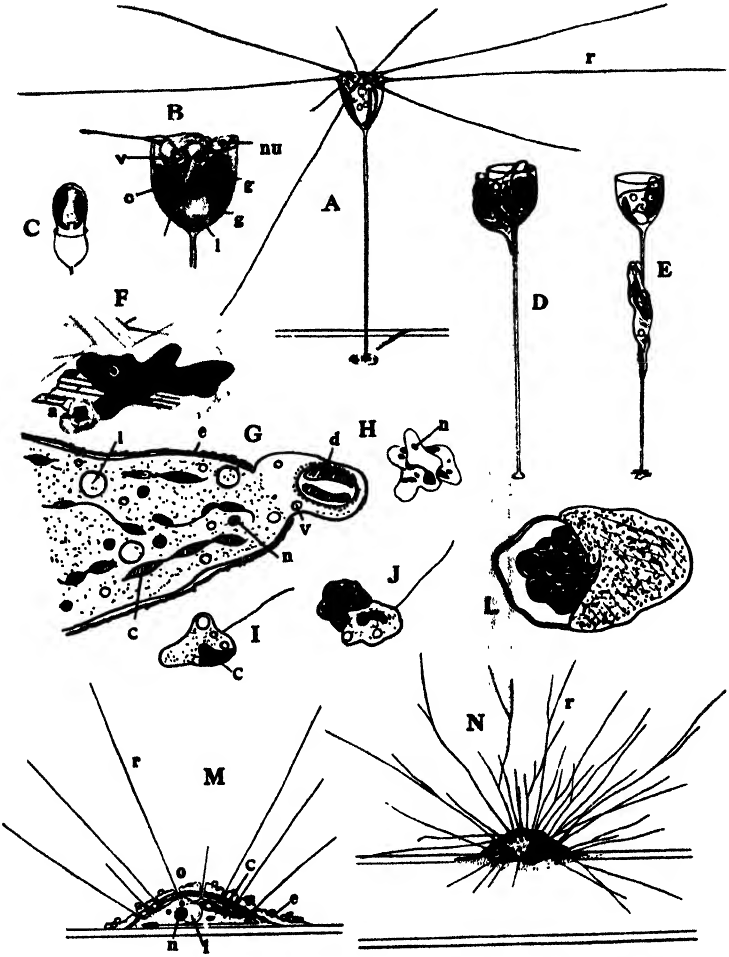

Fig. 177. A–E, *Rhizaster crinoides* Pascher; A, diagrammatic representation; B, apex enlarged to show structure of protoplast; C, cyst; D, E, multiplication, the protoplast has divided and one half has escaped as an amoeba which is progressing down the stalk. F–L, *Myxochrysis paradoxa* Pascher; F, plasmodium which has absorbed a *Scenedesmus* at *a*; G, part of a plasmodium showing chromatophores (*c*), nuclei (*n*), contractile vacuoles (*v*), and leucosin (*l*), also a large pseudopodium engulfing a diatom (*d*); H, swarmer giving rise to a multinucleate plasmodium; I, swarmer; J, escape of same from cyst; L, encysted plasmodium with numerous cysts. M, N, *Chrysocrinus hydra* Pascher; M, in section; N, external view. *c*, chromatophores; *e*, envelope; *g* (in B), inclusions of unknown nature; *l*, leucosin; *n*, nuclei; *nu*, nutritive vacuole; *o* (in M), aperture in envelope; *r*. rhizopodium; *v*, contractile vacuole. (All after Pascher.)

without (fig. 177 J) previous division of the contents, *Chromulina*-like swarmers (fig. 177 I) which may or may not possess a chromatophore and which after some time lose their flagellum and become amoebae; sometimes, however, the swarming stage is suppressed and the amoebae are produced at once. The latter grow and their nuclei divide and sooner or later they form the characteristic envelope; but at all stages of their development fusions can take place and there thus result the large plasmodia that constitute the normal vegetative condition. It seems that sometimes the swarmers or amoebae may arise direct by division of the plasmodia without the above-mentioned encystment occurring. The formation of colourless swarmers and from them of colourless plasmodia depends on the fact that, in the division of the protoplasm, some of the products receive no chromatophores.

The examples cited are sufficient to show that among Chrysophyceae we can trace a practically complete series of transitions to rhizopodial and plasmodial organisation. Commencing with forms like *Chrysamoeba*, where the rhizopodial condition, as in *Heterochloris*, is only a temporary phase, we pass to others (*Chrysopyxis*, Cyrtophoraceae), where the flagellate individual is produced only in relation to reproduction, and from these again to the permanently rhizopodial forms, where flagellate stages may be altogether suppressed. A last step, involving the loss of chromatophores, would bring us to typical Rhizopods which, unless they retained some characteristic assimilatory product or other distinctive feature (e.g. the cyst), would no longer be recognisably derivable from the Chrysophyceae.

The Colourless Forms among Chrysomonadineae (Monadaceae) and Rhizochrysidineae

Among the Chlorophyceae there occur in many groups colourless forms that are quite plainly related to the pigmented types. Forms with reduced and pale-coloured chromatophores are known in *Ochromonas* (e.g. *O. granulosa* (77); cf. also *Chrysococcus tesselatus* (31)) and both here and in *Chromulina* colourless species occur; similarly *Mallomonas apochromatica* Conrad (18) lacks chromatophores. We owe mainly to Scherffel (122, 123) and to Pascher (94, 106) the demonstration of the fact that the Monadaceae (*Monas*, *Stokesiella*, *Physomonas*, etc.), hitherto classed in the group of colourless Flagellates known as Protomastigineae (cf. p. 746), are in large part, if not entirely, colourless Chrysophyceae referable to the Ochromonadeae (cf. also (1), (24)). This is mainly based on their possession of the characteristic cysts (116), (123) (fig. 178 B–D), whilst in several cases leucosin is present as well.

The species of *Monas* (fig. 178 A) closely resemble *Ochromonas*, having the same delicate periplast admitting of change of shape, the

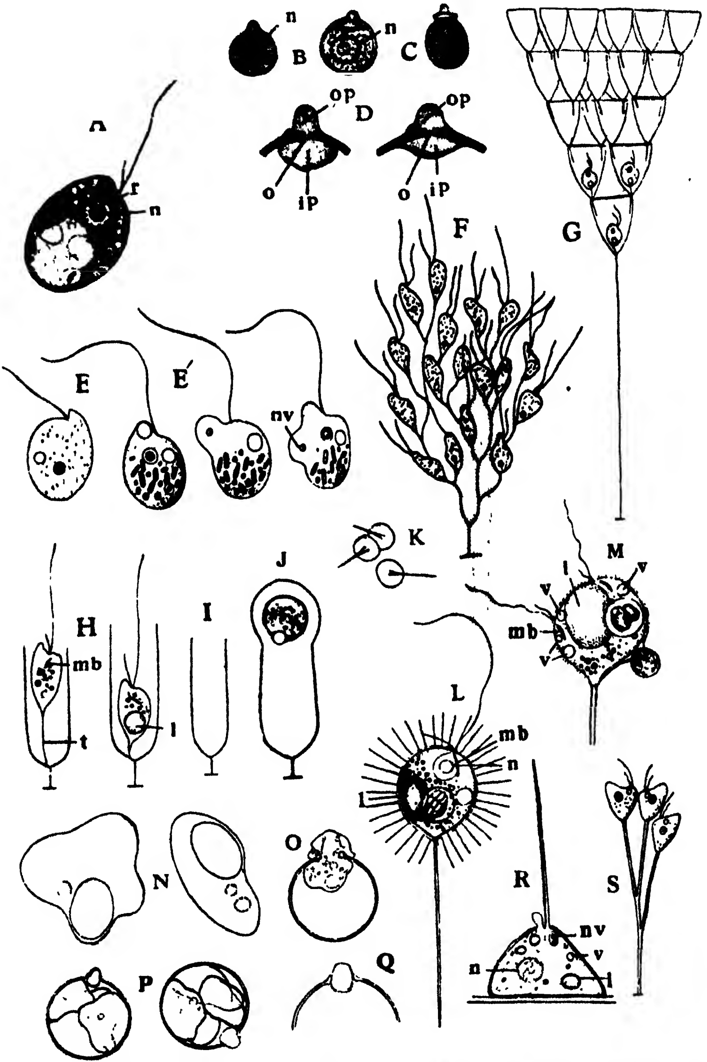

Fig. 178. Colourless Chrysophyceae. A–D, *Monas vulgaris* (Cienk.) Senn; B–D, structure of cysts. E, *Oicomonas socialis* Moroff, free-swimming cell. E′, *O. termo* (Ehrenb.) Kent, holozoic nutrition. F, *Dendromonas laxa* (Kent) Blochm. G, *Stylobryon Abbotii* Stokes. H–J, *Stokesiella epipyxis* Pascher; H, two individuals, that on the right contracted; I, empty envelope;

same unequal flagella arising from an emarginate anterior end, and the same tendency for temporary attachment by means of a thread-like pseudopodium at the posterior extremity (p. 529). In *M. sociabilis* Meyer (77) spherical colonies may be formed. Leucosin is often present and cysts have been found in a number of species. Some species of the uniflagellate *Oicomonas* (Oicomonadaceae, fig. 178 F, E′) have also been found to possess these characteristics (122) and should therefore be transferred to Chrysophyceae as colourless Chromulineae. Both Chadefaud (8) and Gavaudan (34) record forms of *Monas* possessing colourless plastids with apposed eye-spots and those described by the former are stated to have a yellow-green colour.

In describing a new species of the genus, Pascher (106) shows very clearly that *Stokesiella* ((71) p. 373) is a colourless encapsuled type closely related to the section *Epipyxis* of *Dinobryon*. The protoplast has the same structure, with a large posterior lump of leucosin (fig. 178 H). The rather coarse envelope of Pascher's form is composed of successive thimble-shaped pieces fitted into one another, and cysts of the normal Chrysophycean type are formed in just the same way as in *Dinobryon* within a spherical vesicle at the aperture of the envelope (fig. 178 J). The stigma present in a few species of *Monas* and *Stokesiella* is regarded by Scherffel and Pascher as representing the last remnant of the chromatophore. *Stylobryon* (54 *b*, 71, 142), a dendroid *Stokesiella* (fig. 178 G), is in all probability a colourless parallel to the colonial *Dinobryons*, while *Dendromonas* (54 *b*, 71, 139) is so like a colourless *Chrysodendron* (fig. 178 F, S) that one can scarcely doubt that future investigation will confirm the suggestion of a close affinity. Of a similar nature are *Cephalothamnion* (54 *b*, 71, 139) and *Anthophysa* (139), although here the individuals occur in groups at the ends of the branched stalks.

Korschikoff (61) has recently produced evidence that *Physomonas* (fig. 178 L, M), another genus of the Monadaceae (54 *b*, 140, 142) that occurs as a stalked epiphyte, is likewise a colourless member of Ochromonadeae. He has observed probable leucosin masses and the characteristic cysts. The periplast is here covered with small siliceous

J, cyst-formation. K–M, *Physomonas vestita* Stokes; K, discs with bristles from envelope; L, stalked individual; M, beginning of division. N–Q, *Leukochrysis* sp.; N, two amoebae; O, escape of amoeba from cyst; P, division of contents of cysts; Q, upper part of cyst. R, *Heterolagynion Oedogonii* Pascher. S, *Dendromonas virgaria* (Weisse) Stein. *ip*, *op*, inner and outer plugs of cyst respectively; *l*, leucosin; *mb*, mouth-band; *n*, nucleus; *nv*, nutritive vacuole; *o*, aperture of cyst; *r*, rhizoplast; *t*, contractile thread; *v*, contractile vacuole. (A after Alexeieff; B–D after Scherffel; E after Moroff; E′, G, S after Lemmermann; F after Kent; K–M after Korschikoff; the rest after Pascher.)

scales[1] each bearing a long bristle (fig. 178 K), a structure recalling that of *Mallomonas*, although *Physomonas* has the two unequal flagella of other Monadaceae. The cells readily separate from the stalk as amoeboid swarmers which can divide during movement.

Most Monadaceae show near the anterior end of the cell a linear or somewhat curved, strongly refractive band, known in German terminology as the "Mundleiste" (mouth-band, fig. 178 H, L, M, *mb*), although it is certainly not of the nature of a mouth. Its significance and function are altogether obscure. According to Korschikoff it is closely applied to the nucleus in *Physomonas*, and during division a second mouth-band is formed *de novo* on the one daughter-individual. A similar structure is known to occur in many of the pigmented forms (cf. e.g. (50)).

It is not surprising that, among these colourless types, the same amoeboid and rhizopodial tendencies should be manifest as among the pigmented ones. Pascher ((97) p. 43) records such a case for a species of *Monas*, whilst *Heterolagynion* (90) (fig. 178 R) is a colourless parallel of *Lagynion*.[2] The same author has, moreover, described a colourless amoeba, *Leukochrysis* (97) (fig. 178 N), whose inclusion in this class is confirmed by its occasionally forming the characteristic cysts (fig. 178 O–Q).

The colourless members of Chrysophyceae appear to have originated in two ways. In such a form as *Rhizochrysis* the chromatophores do not always divide at the same rate as the protoplasts, with the result that some of the individuals receive none (cf. fig. 176 D and also *Myxochrysis*). According to Pascher ((97) p. 43), however, such colourless individuals do not usually possess much vitality (cf. also (26)). He is of the opinion that colourless forms more usually arise by progressive reduction of chromatophores, as is well shown among Chlamydomonadaceae (p. 90), and for which there is also evidence among Chrysomonadineae (cf. p. 538). Progressive reduction of chromatophores in Chrysophyceae that are acquiring amoeboid or rhizopodial organisation is only too likely to occur in relation to increasing capacity for holozoic nutrition.

(*c*) THE PALMELLOID TYPE (CHRYSOCAPSINEAE)

The not infrequent palmelloid stages recorded in *Chromulina*, *Ochromonas*, *Mallomonas* (15), etc., point the way to the Chrysocapsineae. Pascher (100) enumerates a considerable number of genera with

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[1] The account given by Reynolds (117*a*), who is evidently unfamiliar with Korschikoff's paper, omits all reference to these scales.

[2] *Actinomonas* (71), usually referred to Pantostomatineae (p. 750), may lose its flagellum in the sedentary stage and become altogether rhizopodial ((97) p. 71); this form occasionally produces leucosin and is probably a Chrysomonad.

palmelloid organisation to which others have since been added. In classifying these forms it is difficult to assess the value to be attributed to the characters of the swarmers. Thus, the genus *Chrysocapsa* (36, 39, 91), with small spherical or ellipsoidal gelatinous colonies which are free-floating or attached (fig. 179 A, B), includes forms with motile stages possessing either one or two flagella. Pascher ((100) p. 550) suggests restricting the genus to forms with uniflagellate swarmers, an attitude that in the present state of our knowledge appears warranted, although on this basis very similar forms will be distinguished almost solely by the mode of flagellation of their motile stages.

In *Chrysocapsa* (fig. 179 A, B) the mucilage is structureless, whilst in *Gloeochrysis* ((100) p. 550) it exhibits stratification around the individual cells (fig. 179 E), after the manner of a *Gloeocystis*. The cells of *Gloeochrysis* (fig. 179 G) contain a single large parietal chromatophore with an embedded pyrenoid-like body (*p*) which is highly refractive. The swarmers (fig. 179 F) are uniflagellate and resemble a *Chromulina*. Conrad's *Pascherella* ((17) p. 221), found in brackish water, has numerous cells which possess the reticulate chromatophore (fig. 179 K) of a *Chrysapsis* (p. 514) embedded in mucilage showing some stratification. Multiplication is effected by swarmers (fig. 179 L) with a very long flagellum. In these diverse forms contractile vacuoles are frequently recognisable in the palmelloid phases and in *Gloeochrysis* and *Pascherella* a stigma is often present as well (fig. 179 G, K).

West's *Phaeosphaera* (145), at present only recorded from *Sphagnum*-bogs in Cornwall, has the large spherical cells, with a single parietal chromatophore, embedded in a little-branched gelatinous cylinder (fig. 179 C, D); the reproduction is unknown. In *Phaeocystis* (7, 46, 65, 119) and *Phaeogloea* (10) the multiplication takes place with the help of ochromonad swarmers (fig. 179 I) with two unequal flagella. The former is not uncommon in marine plankton and occurs as large spherical lobed colonies (fig. 179 H) which reproduce also by detachment of the lobes.

All of these forms, which may for the present be classed as Chrysocapsaceae, are imperfectly known and in want of detailed study. A rather more specialised member of this family is *Celloniella* found by Pascher (104) attached to rocks in rapid alpine streams. Where the flow is not torrential, *Celloniella* appears as foliose, lobed, gelatinous expanses composed of very delicate mucilage in which the cells are disposed mainly at the periphery (fig. 180 A, E); below, the colony narrows to a rounded or flattened stalk-like portion with firmer mucilage, while in the basal attaching disc the latter is cartilaginous, markedly stratified and encrusted with carbonate of lime. On the rocks of cataracts only this flat stratified basal crust is formed, whilst

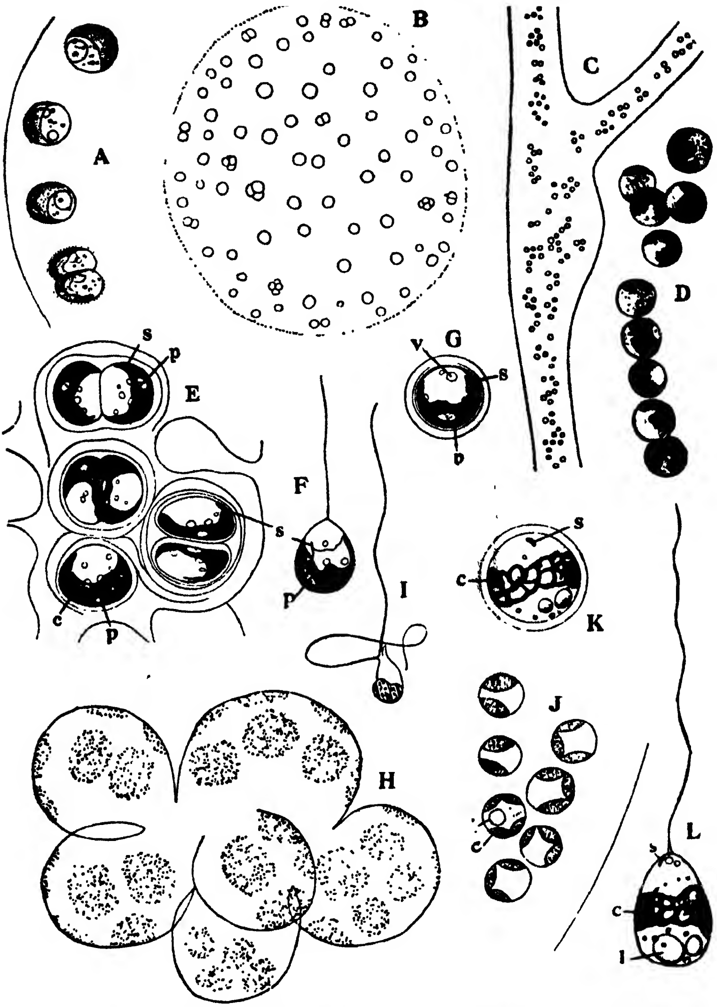

Fig. 179. Palmelloid Chrysophyceae (Chrysocapsineae). A, B, *Chrysocapsa planctonica* Pascher; A, edge of a colony. C, D, *Phaeosphaera gelatinosa* West; D, a number of the cells enlarged. E–G, *Gloeochrysis pyrenigera* Pascher; E, part of stratum; F, swarmer; G, the same after coming to rest. H–J, *Phaeocystis Poucheti* Lagerh.; I, swarmer; J, group of cells enlarged. K, L, *Pascherella Yserensis* Conrad; K, single cell from a colony; L, swarmer. *c*, chromatophore; *l*, leucosin; *p*, pyrenoid; *s*, stigma; *v*, contractile vacuole. (C, D after West; H, J after Lagerheim; I after Pouchet; K, L after Conrad; the rest after Pascher.)

in sheltered situations not exposed to the current the colonies develop as vesicular or racemose masses. At the apices of the lobes of the normal form the cells, elsewhere mainly in a single layer, are irregularly heaped together (fig. 180 B, E), and these are the main centres of growth where abundant division occurs. The cells possess a single chromatophore and a contractile vacuole (fig. 180 B), and can escape as *Chromulina*-like amoeboid swarmers (fig. 180 F, J) devoid of a stigma. These swarmers can multiply by division during the motile phase. Characteristic cysts (fig. 180 C, D), provided with curved longitudinal ridges, have been found within the mucilage.

Pascher (109) has also described a subaerial form, *Geochrysis*, which occurs on peaty soil as olive-green or greenish black, extensive gelatinous strata containing numerous cells with the usual single chromatophore and a contractile vacuole. Reproduction is effected by uniflagellate swarmers and by breaking up of the stratum into single cells or groups of cells which are enveloped in thick gelatinous envelopes and are dispersed by the wind (fig. 180 L, N, O).

A curious freshwater epiphyte *Naegeliella* (23, 45, 124), first described by Correns, is placed by Pascher ((100) p. 560) in a special family Naegeliellaceae. It forms small rounded discs, at first one-layered, later several-layered in the middle, attached to diverse aquatics (fig. 180 H, I). The cells, which contain a deep yellow-brown chromatophore and a number of contractile vacuoles (fig. 180 M), are embedded in mucilage which forms a thick envelope on the side away from the substratum. The peculiar feature of the alga lies in the presence of one or more richly branched mucilage-bristles which arise from the upper surface of the disc and may attain to considerable length (fig. 180 G, I, *h*). In the form described by Correns (*N. flagellifera* (23)) they develop in the following way.

The swarmer, after settling down on a substratum, secretes a mucilage-envelope from the inner part of which a hair (*h*) is protruded, the ruptured outermost layer forming a loose sheath (fig. 180 K, *m*) around its base. When the cell divides, the inner part of the newly formed mucilage-envelope around each daughter-cell grows out into a similar hair which extends into the soft central mucilage of the primary bristle and, bursting the apex of the latter, projects into the water (cf. fig. 180 K, *s*). Since this series of events is repeated time after time, a tuft of bristles arising from a common sheath and becoming free at diverse levels gradually arises. By degrees the oldest bristles ensheathing the younger ones are burst open and thus two, and later several, separate multiple bristles are formed. Since these elongate structures are flexible they appear on old colonies as a convoluted mass of threads which are often entangled with one another. This method of forming mucilage-hairs is unique.

In the forms described by Scherffel (124) and Godward (45) the bristles

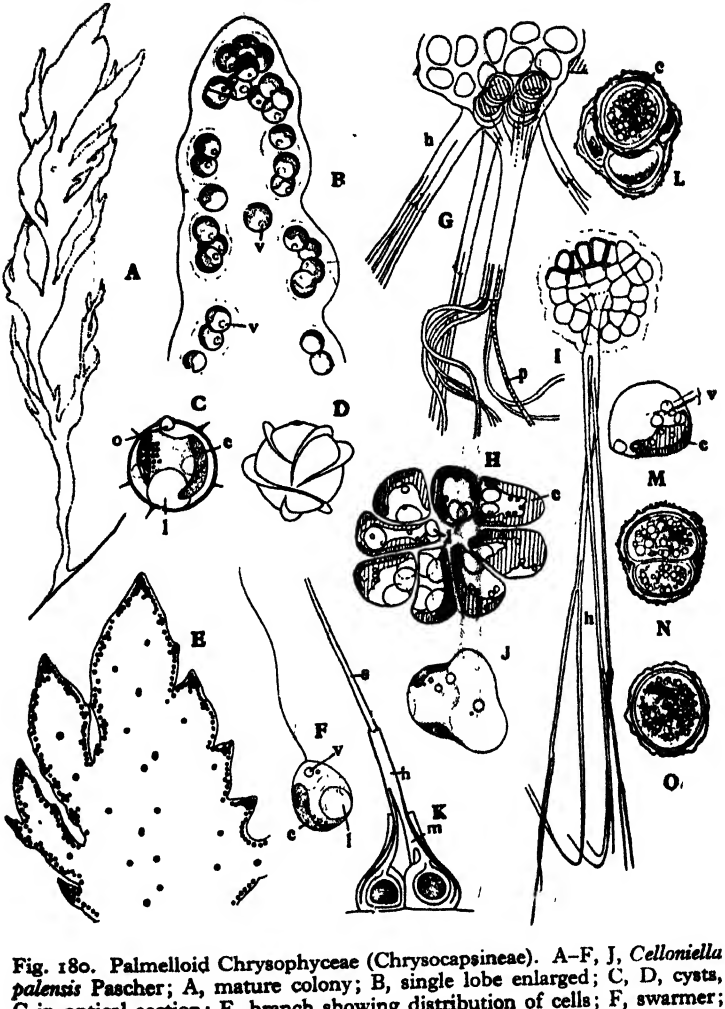

Fig. 180. Palmelloid Chrysophyceae (Chrysocapsineae). A–F, J, *Celloniella palensis* Pascher; A, mature colony; B, single lobe enlarged; C, D, cysts, C in optical section; E, branch showing distribution of cells; F, swarmer; J, amoeboid stage of same. G–I, M, *Naegeliella britannica* Godward; G, colony with several bristles; H, young colony seen from above; I, colony with a single bristle; M, single cell. K, *N. flagellifera* Correns, small colony in optical section. L, N, O, *Geochrysis turfosa* Pascher, single cells or cell-groups; in L only one cell of the group alive. *c*, chromatophore; *h*, mucilage-hair; *l*, leucosin; *m*, mucilage; *o*, plug of cyst; *p*, protoplasmic thread; *s*, secondary bristle; *v*, contractile vacuole. (G–I, M after Godward; K after Correns; the rest after Pascher.)

contain delicate threads of cytoplasm continuous with the protoplasts of the cells of the disc (fig. 180 G, *p*), so that in these cases the structures in question are quite comparable to the pseudocilia of Tetrasporaceae, except for the fact that several are combined to form a branched compound structure. In the main branches a considerable number of cytoplasmic threads are recognisable, but the ultimate branches contain only a single one. It is unlikely that Correns, the discoverer of pseudocilia in the Tetrasporaceae, overlooked them in his species of *Naegeliella*, and at present it appears that there may be a number of different forms, some with and some without cytoplasmic threads in the bristles.

Correns recorded swarmers with two laterally attached flagella formed directly from the cells of the disc.

The highest development among the Chrysocapsineae is found in *Hydrurus*[1] (Hydruraceae), an inhabitant of cold streams, which in its marked division of labour far surpasses any of the palmelloid forms found in other classes and may in some respects be ranked as high as *Draparnaldia*. The only species, *H. foetidus* (Vill.) Kirchn., occurs as richly branched, olive-green, feathery tufts (fig. 181 A), 1–30 cm. long, sticky to the touch and giving off an offensive odour when alive; they are occasionally encrusted with carbonate of lime. The plant is composed of tough, almost cartilaginous, cylindrical mucilage-strands, said to contain callose (144), in which are embedded the numerous naked cells. These are at first spherical, later ellipsoidal or pear-shaped (fig. 181 B, F). In each strand the cells are densely aggregated at the periphery and more loosely disposed in the central portion (fig. 181 F). A single curved chromatophore (*c*), containing a pyrenoid-like body (*p*) (cf. also fig. 166 H) is apposed to the anterior, often pointed and upwardly directed end of the cell (fig. 181 C, E), whilst the broad downwardly directed part contains a number (5–6) of contractile vacuoles (*v*) and lumps of leucosin.

Each branch grows apically (fig. 181 B), the end-cell undergoing repeated longitudinal division, one half reconstituting the "apical cell", the other contributing to the lengthening of the branch; new branches arise mainly in acropetal succession. The mucilage seems to be secreted largely by the posterior end of the cell. The formation of swarmers is stated to be confined to the short branches and ensues after longitudinal division of series of cells. The swarmers are uniflagellate and tetrahedral in shape, the front end being drawn out into three slightly amoeboid processes, while the back end with the chromatophore is pointed (fig. 181 G). The swarmers become attached by their anterior end and immediately secrete a mucilage-cylinder (fig. 181 C), within which longitudinal division of the protoplast (fig. 181 E) soon commences; gradually certain of the peripheral cells take on the functions of apical cells and produce branches.

[1] See (2), (37), (56), (57), (64), (118).

Cyst-formation occurs during the summer months in certain cells which are carried out in mucilage-strands beyond the general surface (fig. 181 J), after which a silicified membrane with the customary pore and plug is secreted within each. The mature cysts are biconvex, with a broad delicate wing extending round half the periphery (fig. 181 H, I). Palmella-stages have also been recorded, but are

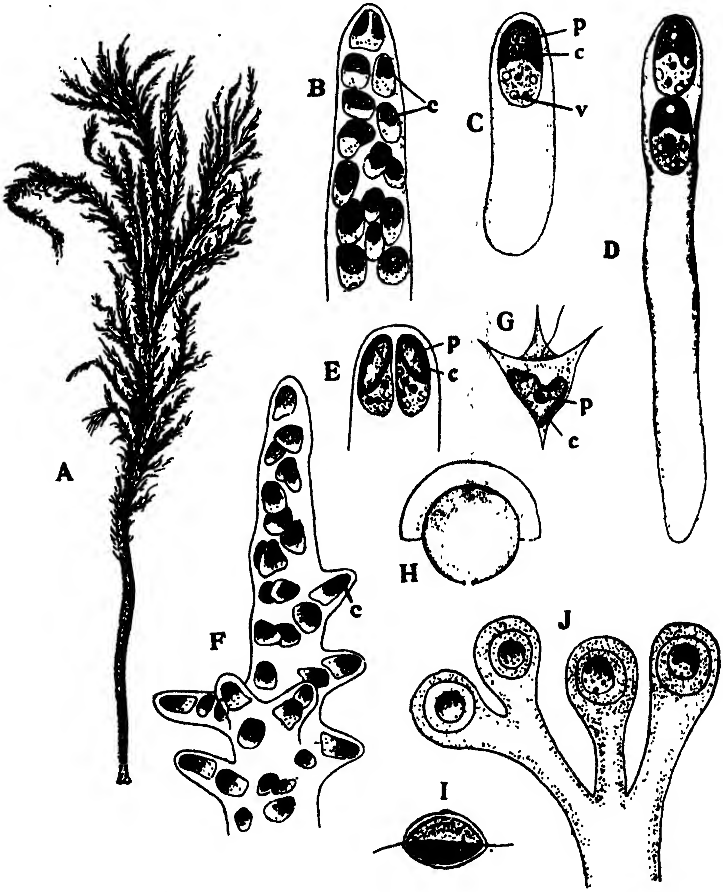

Fig. 181. *Hydrurus foetidus* (Vill.) Kirchn. A, habit; B, apex of a mature colony; C–E, early stages of development; F, apex of a colony showing branching; G, swarmer; H, I, cysts, in H from the surface, in I from the side; J, branch with cysts. *c*, chromatophore; *p*, pyrenoid; *v*, contractile vacuole. (A after Rostafinski; F after Berthold; the rest after Klebs.)

imperfectly known. It is remarkable that this highly specialised form should have naked cells and that sexual reproduction has so far not been observed.

It will be evident from the preceding description that the palmelloid types among Chrysophyceae attain to a higher differentiation than among either Chlorophyceae or Xanthophyceae.

Order II. *CHRYSOSPHAERALES*

These are the Chrysophycean forms parallel to Chlorococcales and Heterococcales and include a number of types with firm cell-walls of unknown composition. It is noteworthy that none of the Chrysosphaerales so far discovered form well-defined colonies such as occur abundantly in Chlorococcales.

Chrysosphaera ((100) p. 533), the first form to be described (92), possesses relatively large spherical cells (fig. 182 A) which contain a pair of parietal yellowish-brown chromatophores (*c*), as well as drops of oil (*o*) and often large lumps of leucosin (*l*). The cells multiply by division of the protoplast, the halves forming new membranes of their own and remaining for a time within the stretched parent-membrane, so that four-celled aggregates may be formed. The divided protoplasts can, however, escape as uniflagellate swarmers (fig. 182 B) provided with two anterior contractile vacuoles and an eye-spot.

Epichrysis ((39), (78), (100) p. 538; including *Phaeocapsa paludosa* Korschikoff (59a)) occurs as an epiphyte on filamentous freshwater Algae, often appearing in dense clusters (fig. 182 C) in which the cells are flattened as a result of mutual pressure. The isolated cells (fig. 182 D) are spherical and contain a single chromatophore, mostly apposed to the outer side of the cell, whilst oil-drops and leucosin are usually present. Multiplication is effected as in *Chrysosphaera* (fig. 182 D, E). Pascher reports that when the protoplasts divide, whether to form swarmers or not, a pair of contractile vacuoles (*v*), usually appear in the resulting cells. This shows that division here (as also in *Chrysosphaera*) is only to be regarded as a case of suppressed swarmer-formation. The uniflagellate swarmers (fig. 182 E, E′) can also give rise to free-floating palmelloid stages, within which typical Chrysophycean cysts may be formed.

Schiller ((126), (128) p. 67) has described a marine member of this order, *Aurosphaera* (fig. 182 K) possessing a silicified membrane bearing silicified bristles attached to scales as in *Mallomonas* and reproducing by uniflagellate swarmers or autospores. Another marine form is Geitler's ((40) p. 629) *Sarcinochrysis*, found in marine cultures from the Canary Islands. This form (fig. 182 M) occurs as cubical packets of rounded cells with a pair of yellowish lobed parietal chromatophores and surrounded by a delicate membrane. The swarmers, formed directly from the protoplasts without previous division, are oblong with an obliquely truncated anterior extremity from a slight depression in which arise two flagella of unequal length, the longer directed forwards, the shorter being dragged behind (fig. 182 L). As Geitler points out, the type of swarmer is unusual among Chrysophyceae and recalls to some extent that of Phaeophyceae. In how far this difference is significant further research must show.

Chodat has applied the name Chrysostomataceae ((10) p. 81) to a

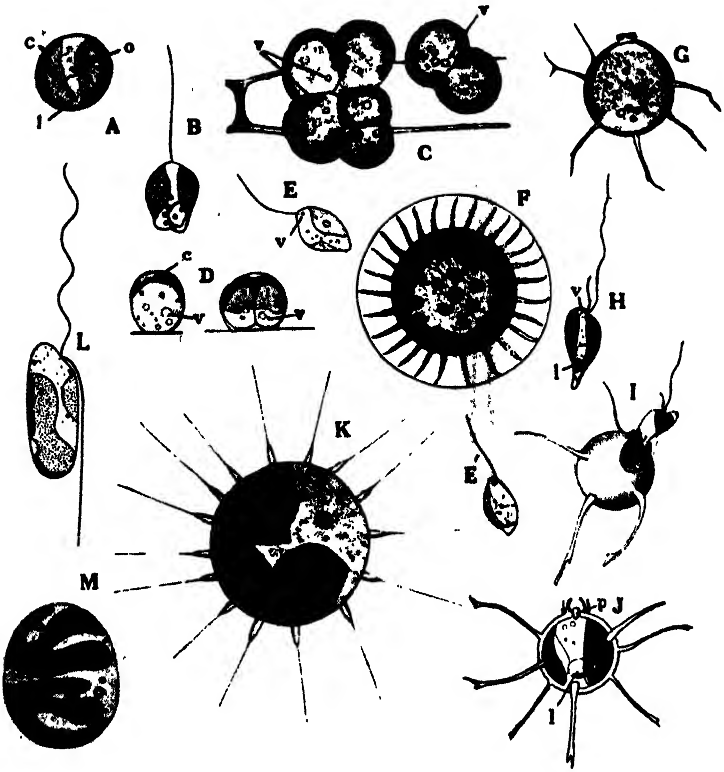

Fig. 182. Chrysosphaerales. A, B, *Chrysosphaera nitens* Pascher; B, swarmer. C–E, *Epichrysis paludosa* (Korschik.) Pascher; C, group of cells on *Tribonema*; D, single cell and division-stage; E, E′, swarmers. F, *Pterosperma Joergensenii* Schill. G, *Chrysostrella paradoxa* Chod. H–J, *Echinochrysis Chodati* Conrad; H, swarmer; I, liberation of same; J, ordinary cell. K, *Aurosphaera echinata* Schill. L, M, *Sarcinochrysis marina* Geitl.; L, swarmer from the side; M, single cell. *c*, chromatophore; *l*, leucosin; *o*, oil; *p*, plug; *v*, contractile vacuole. (C after Korschikoff; F, K after Schiller; G after Chodat; H–J after Conrad; L, M after Geitler; the rest after Pascher.)

series of unicellular freshwater forms, closely resembling the siliceous cysts produced by members of this class (e.g. *Chrysostrella*, fig. 182 G). They may represent a separate line of Chrysosphaerales in which such resting stages have become the normal vegetative condition, but their status is not yet clear (cf. (10) p. 82, (11), (100) p. 547) and many will probably prove to be the cysts of other members of the class. Conrad ((17) p. 222) has, however, described a genus, *Echinochrysis* (fig. 182 J), which reproduces by swarmers of the *Ochromonas*-type (fig. 182 H, I), and which appears to establish the independent existence of such forms.

Another group of doubtful organisms belonging here are the marine *Pterospermaceae* (cf. (73 *a*), (128) p. 72), some of which may well be specialised members of Chrysosphaerales. The forms in question have spherical cells with a firm membrane provided with one (fig. 182 F) or more wings placed perpendicular to the surface and strengthened by ridges; the cells contain numerous brown discoid chromatophores.

Order III. *CHRYSOTRICHALES*

Perhaps one of the most striking contributions to our knowledge of this class in recent years has been the description of a number of filamentous forms, among which the genus *Phaeothamnion* (63) appears at length to have found a secure resting-place. Although the relevant forms are not numerous and appear to be of restricted distribution, their discovery shows more plainly than anything else that the Chrysophyceae have followed the same evolutionary trend as other classes with flagellate representatives in respect of the differentiation of true plant-forms.

The simplest type is represented by *Nematochrysis* ((100) p. 511; first described as *Chrysothrix* (92)), so far only found in salt water. This possesses simple unbranched filaments, attached by a basal cell with scanty contents and thick stratified walls (fig. 183 A, B). Apart from this all the cells are alike, cylindrical or barrel-shaped in form, with two parietal chromatophores (*c*) and the clear cytoplasm usual in Chrysophyceae; there are also drops of oil (*o*) and leucosin-masses (*l*). As in other Chrysotrichales the threads readily pass over into a palmelloid condition, the cells rounding off and the membranes becoming gelatinous, while at such times the protoplasts often develop eye-spots. This indicates that, as in other filamentous series, the palmelloid phase represents but a modification of the ordinary process of swarmer-formation. The cells in these palmelloid stages readily form cysts, thin-walled but otherwise typical.

Biflagellate swarmers (fig. 183 I), provided with a stigma (*s*) but without contractile vacuoles, are usually formed from the cells without division. They are markedly metabolic and escape through an aperture formed in the side wall, the posterior end of the swarmer emerging first. On coming to rest they give rise to an almost spherical cell, whose membrane adjacent to the substratum becomes prominently thickened (fig. 183 C, D). The first, as well as all later, divisions of the protoplasts are oblique (fig. 183 C, D, F), but, before the daughter-protoplasts secrete their own membranes, the plane of separation

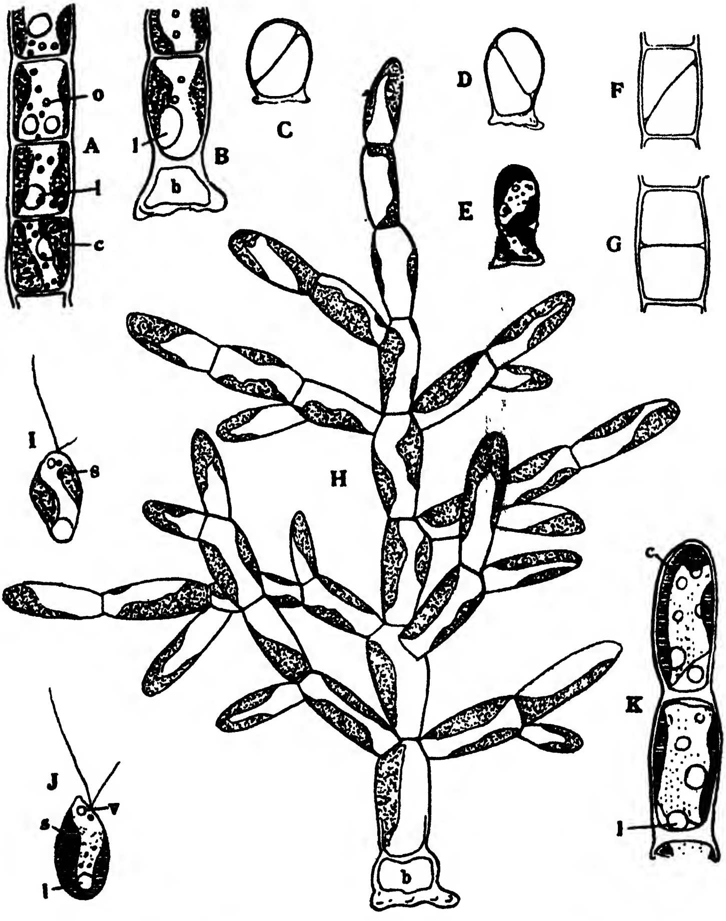

Fig. 183. Chrysotrichales. A–G, I, *Nematochrysis sessilis* Pascher; B, basal portion of a thread; C, D, unicellular plant, division of protoplasts; E, two-celled stage; F, G, successive stages in division of a cell of the thread; I, swarmer. H, *Phaeothamnion confervicolum* Lagerh., habit. J, K, *P. Borzianum* Pascher; J, swarmer; K, apex of a branch. *b*, basal cell; *c*, chromatophore; *l*, leucosin; *o*, oil; *s*, stigma. *v*, contractile vacuole. (All after Pascher.)

becomes transverse (fig. 183 E, G). The lower cell formed from the germinating swarmer undergoes no further division and gradually assumes the mature form of the basal attaching cell, while the upper segments divide to form the thread.

Phaeothamnion ((45), (63), (100) p. 498), probably not uncommon in freshwaters in the colder period of the year, develops short, branched (fig. 183 H) or sometimes unbranched filaments, attached to other water-plants by a thick-walled basal cell (*b*) like that of *Nematochrysis*. The cells are cylindrical and have firm cellulose walls, which are sometimes stratified and readily become mucilaginous; they contain either a single lobed parietal chromatophore (*P. confervicolum*; cf. fig. 183 H, K) or several discoid ones (*P. polychrysis*), apart from the usual inclusions of the Chrysophycean cell. All the cells, except for the basal one, are capable of division, but in older plants those of the main axis lose this capacity. The method of segmentation is similar to that above described for *Nematochrysis*, but the plane of division is not so markedly oblique.

The swarmers (fig. 183 J) resemble those of *Nematochrysis* and are formed to the number of one or two (rarely 4–8) in a cell, being liberated through a lateral aperture and being sometimes temporarily enveloped in a vesicle. They either give rise directly to new filaments or round off and divide repeatedly to form palmelloid stages (fig. 184 F) which, as in *Nematochrysis*, can also originate directly from the ordinary filaments (fig. 184 A). The cells of such palmelloid stages may later produce zoospores or form typical Chrysophycean cysts, liberating one or two swarmers on germination. Pascher ((100) p. 504) mentions that the swarmers often contain a number of highly refractive bodies which disappear during germination and possibly furnish the material for the strong thickening of the basal cell (cf. Xanthophyceae, p. 492). Borzi ((6) p. 454) recorded sexual reproduction, but this remains very doubtful.

Hansgirg's *Phaeodermatium* ((47) p. 207) forms more or less circular discs (fig. 184 B), sometimes attaining considerable dimensions, on the rocks of cold, especially calcareous streams. These crusts are one-layered at the margin, but composed of several layers in the centre (fig. 184 E, I) and at first show clearly their origin from coalescent filaments; in older plants this filamentous structure is more or less obscured. Pascher ((100) p. 518) described how some of the marginal threads may elongate markedly like runners and give rise at their apices to secondary crusts. The cells possess the usual parietal lobed chromatophore and contain oil and leucosin, while the membrane of older cells is often brownish and distinctly stratified.

At times the cells round off with gelatinisation of the membranes and the protoplasts of such palmelloid stages occasionally develop contractile vacuoles. They readily form swarmers which are of course

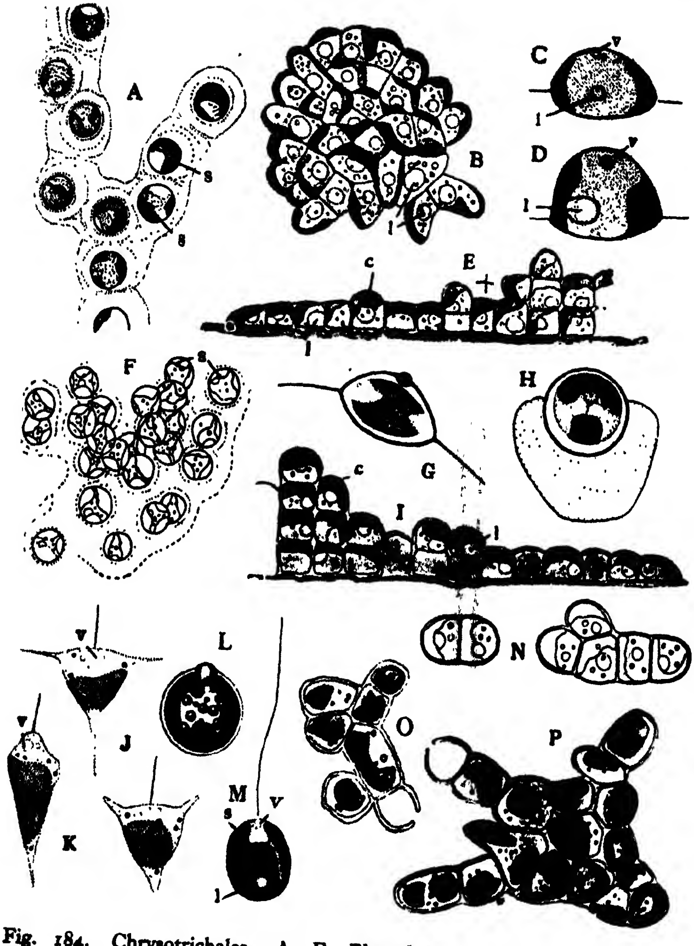

Fig. 184. Chrysotrichales. A, F, *Phaeothamnion Borzianum* Pascher, palmelloid stages. B–E, G–K, N, *Phaeodermatium rivulare* Hansg.; B, a young one-layered disc; C, D, germinating swarmers; E, semi-diagrammatic section of an older crust, at + an erect thread is forming a horizontal branch; G, side- and H, surface-views of cysts; I, radial section of a mature stratum; J, K, three swarmers, the one on the left showing metaboly; N, young plants. L, M, O, P, *Thallochrysis Pascheri* Conrad; L, cyst; M, swarmer; O, P, two plants, both with cells that have liberated swarmers. *c*, chromatophore; *l*, leucosin; *s*, stigma; *v*, contractile vacuole. (G, H, J, K after Geitler; L, M–P after Conrad; the rest after Pascher.)

also produced from the cells of the crusts, escaping with the posterior end foremost as in other Chrysotrichales. Here, however, the swarmers (38) are uniflagellate and closely resemble those of *Hydrurus* (fig. 184 J); they are highly metabolic. After a brief period of movement they settle down to form a hemispherical cell (fig. 184 C, D) which spreads out on the substratum and soon divides (fig. 184 N); by further segmentation a branching filament and gradually a parenchymatous disc are formed (fig. 184 B). The several-layered character of the central part results from the upgrowth of vertical few-celled closely apposed branches (fig. 184 I), as in *Pseudopringsheimia* (p. 260) or the red alga *Hildenbrandia*. According to Pascher ((100) p. 525) the cells of these upright threads can also produce horizontal branches (cf. + in fig. 184 E) closely adpressed to the basal stratum, whereby a several-layered condition is likewise attained. As in other members of this order the swarmers can also at times give rise to palmelloid stages. The cysts (fig. 184 G, H), recorded by Geitler (38), are very similar to those of *Hydrurus*.

Phaeodermatium is thus clearly a discoid type based on a heterotrichous filament, and it is not improbable that further research will disclose the existence among the Chrysophyceae of heterotrichous forms with the habit of a *Stigeoclonium* or *Ectocarpus*. The genus *Thallochrysis*, described by Conrad (16, 17) from brackish water, appears as a strongly reduced form of the same general type as *Phaeodermatium*. It occurs as short branched threads or parenchymatous one-layered discs with an obvious filamentous structure which either float freely or are attached to other aquatics (fig. 184 O, P). The cells vary in form, being sometimes more rounded, sometimes polygonal, and are enveloped by a relatively thick membrane which does not appear to contain cellulose; the large chromatophore is as usual parietal. The swarmers (fig. 184 M) are like a *Chromulina* and are formed singly, especially from the end-cells (cf. fig. 184 P). According to Conrad cell-division takes place in three directions, and not uncommonly groups of cells separate off as pleurococcoid aggregates which apparently constitutes a method of vegetative multiplication. Typical cysts are also known (fig. 184 L).

A similar type is constituted by *Apistonema*[1] (108), one species of which has pyrenoids in its chromatophores, while Geitler's *Placochrysis* (36) and Chodat's *Phaeoplaca* (11) are one-layered discoid types without evidence of filamentous structure.

It is perhaps significant that the upright members of the Chrysotrichales have ochromonad swarmers, while in the prostrate types they are of the *Chromulina*-pattern. Pascher ((100) p. 510), however, briefly

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[1] Certain of the stages figured by Borzi (6) as *Phaeococcus Clementi* (cf. p. 659) belong to a species of this genus.

refers to a branched filamentous form, *Chrysoclonium*, in which chromulinoid swarmers are probable.

The Chrysotrichales thus exhibit about the same diversity of development as do the Heterotrichales, although they do not include any such ubiquitous type as *Tribonema*. Further investigation will no doubt widen the range.

STATUS AND TAXONOMY OF THE CHRYSOPHYCEAE

It is clear, however, that the principal development of the Chrysophyceae, as in the case of the Xanthophyceae, centres around the unicell and colony. The relatively slight development in the upward direction is also implied in the simplicity of the reproductive methods and in the apparent scarcity of sexual reproduction. In view of the multiplicity of form among the motile types, it is probable that the class may be in course of active evolution at the present day. So far no siphoneous representatives have come to light.

The affinities of the class are considered at the end of the section dealing with the Bacillariophyceae (p. 642).

The following is an outline of the classification which underlies the preceding matter and which is essentially based on Pascher's scheme (100):

I. *Chrysomonadales:*
  (*a*) *Chrysomonadineae:*
    (i) *Chromulineae:*
      1. *Chromulinaceae:* Chromulina, Chrysamoeba, Chrysapsis, Chrysococcus, Chrysopyxis, Pyramidochrysis.
      2. *Oicomonadaceae* (?, cf. p. 540).
      3. *Mallomonadaceae:* Chrysosphaerella, Conradiella, Mallomonas, Microglena, Pseudomallomonas.
      4. *Cyrtophoraceae:* Cyrtophora, Palatinella, Pedinella.
    (ii) *Isochrysideae:*
      5. *Isochrysidaceae:* Chrysidalis (?), Derepyxis, Syncrypta, Wyssotzkia (?).
      6. *Coccolithophoridaceae:* Acanthoica, Coccolithus, Discosphaera (?), Haplopappus, Hymenomonas, Pontosphaera, Rhabdosphaera (?), Scyphosphaera, Thorosphaera.
      7. *Synuraceae:* Chlorodesmus, Skadovskiella, Synura.
    (iii) *Ochromonadeae:*
      8. *Ochromonadaceae:* Chrysobotrys, Chrysodendron, Cyclonexis, Ochromonas, Uroglena (including Uroglenopsis).
      9. *Monadaceae:* Anthophysa, Cephalothamnion, Dendromonas, Monas, Physomonas, Stokesiella, Stylobryon.
      10. *Lepochromonadaceae:* Diceras (?), Dinobryon, Hyalobryon, etc.
    (iv) *Prymnesieae:*
      11. *Prymnesiaceae:* Prymnesium.

(*b*) *Rhizochrysidineae:*

12. *Rhizochrysidaceae:* Chrysarachnion, Chrysidiastrum, Leukochrysis, Myxochrysis, Platychrysis, Rhizochrysis.

13. *Lagynidaceae:* Chrysocrinus, Heterolagynion, Lagynion, Rhizaster.

(*c*) *Chrysocapsineae:*

14. *Chrysocapsaceae:* Celloniella, Chrysocapsa, Geochrysis, Gloeochrysis, Pascherella, Phaeocystis, Phaeogloea, Phaeosphaera.

15. *Naegeliellaceae:* Naegeliella.

16. *Hydruraceae:* Hydrurus.

II. *Chrysosphaerales:*

17. *Chrysosphaeraceae:* Aurosphaera, Chrysosphaera, Epichrysis, Ochrosphaera (?), Sarcinochrysis.

18. *Chrysostomataceae:* Chrysostrella, Echinochrysis, etc.

19. *Pterospermaceae* (p. 550).

III. *Chrysotrichales:*

20. *Nematochrysidaceae:* Nematochrysis.

21. *Phaeothamnionaceae:* Apistonema, Chrysoclonium, Phaeothamnion.

22. *Thallochrysidaceae:* Phaeodermatium, Phaeoplaca, Placochrysis, Thallochrysis.

THE SILICOFLAGELLATA

Only brief mention can be made of the marine Silicoflagellata,[1] some of which at least are probably related to the Chrysophyceae. The small organisms belonging to the Dictyochaceae are characterised by the possession of a skeleton (fig. 185 A) taking the form of a framework of siliceous rods arranged in diverse ways and with intervening spaces of definite shape. Outside this skeleton (41) is a delicate layer of cytoplasm containing, in *Distephanum speculum* (fig. 185 A) and other forms, a number of bright yellow to brownish yellow discoid chromatophores. According to Hovasse (150), however, the skeleton is external in the adult individual. At the surface there is perhaps a delicate membrane, although Hovasse ((150) p. 478) figures a rhizopodial stage of *Distephanum octonarium*. The spherical nucleus lies in the middle of the cell. Fat appears to occur as an assimilatory product, and leucosin is also stated to be present (150). Apically there is a single flagellum.

The siliceous skeleton may be a simple ring, ellipse (*Mesocena*, fig. 185 H, I), or triangle, but is often much more complex, consisting of two rings or polygons joined by a series of rods (e.g. *Distephanum*, fig. 185 B, C). According to the recent account given by Gemeinhardt (41) the adult individual possesses two of these skeletons (fig. 185 G), more

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[1] See (5), (24*b*), (41), (115*a*) p. 73, (128), (133), (150).

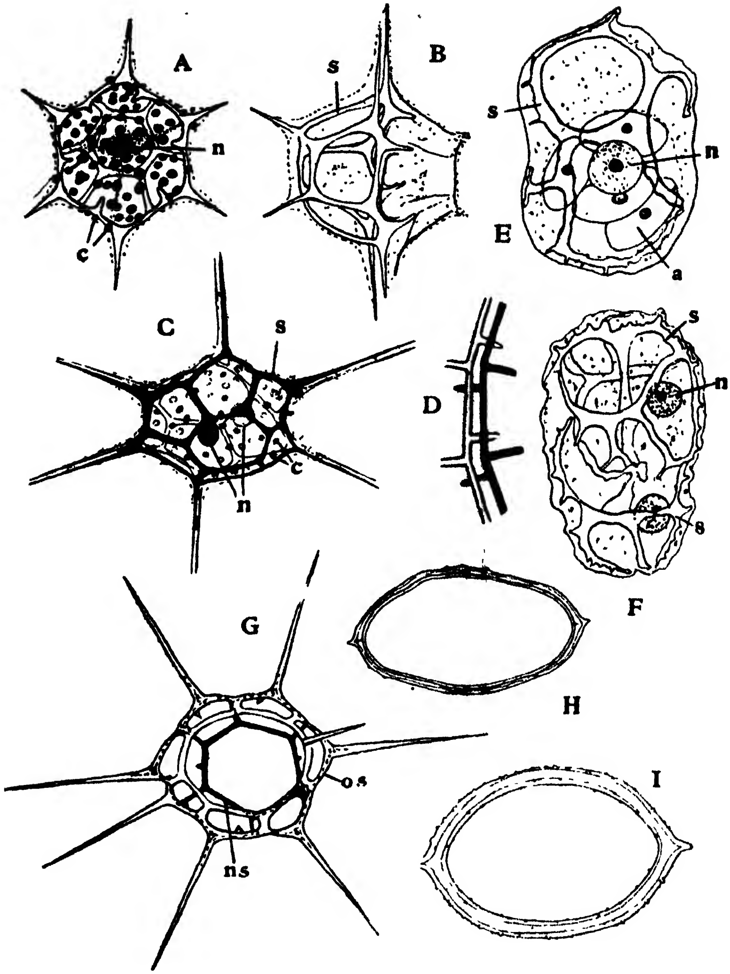

Fig. 185. Silicoflagellata. A–D, G, *Distephanum speculum* (Ehrenb.) Haeckel; A, cell with single skeleton; B, development of second skeleton; C, dividing individual; D, diagram showing relation of the two skeletons; G, individual with the new skeleton (dark) not yet fully differentiated. E, F, ***Ebria tripartita*** (Schum.) Lemm.; E, individual with Zooxanthellae (*a*); F, individual with two skeletons (*s*) and two nuclei (*n*). H, I, *Mesocena crenulata* Ehrenb. var. *diodon* (Ehrenb.) Lemm., skeletons of two individuals. *c*, chromatophore; *n*, nucleus; *ns*, new and *os*, old skeletons; *s*, skeleton. (All after Gemeinhardt.)

or less fitted into one another (fig. 185 D). It appears, however, that the second skeleton is commonly formed only a short time before division (fig. 185 B), the daughter-individuals thus possessing one only during the early periods of their growth. Hovasse (50 b), in confirming this, points out that the new skeleton is a mirror-image of the old one, so that that of the new individual differs from that of the parent, but is like that of the grandparent. Schiller ((128) p. 65), on the other hand, records a process of division affecting only the protoplast, the flagellum of the parent-individual being cast off and each daughter-individual forming one afresh. One or sometimes both daughter-individuals swarm away and form a fresh skeleton. Schiller also records probable resting stages with a distinct membrane and devoid of flagella.

A large number of the species are known only in the fossil condition (42), and, since in most of the living forms, the protoplasmic body is very imperfectly known, the classification is based almost entirely on the characters of the skeleton. The living forms occur at times in large numbers in the plankton, especially in the colder seas. Silicoflagellata have been found from the Cretaceous onwards (133), the older forms being relatively simple with a prevalently triradiate skeleton (*Dictyocha triacantha*); in the later Tertiary more complex forms appear which do not seem to differ materially from those of the present day.

By contrast to the autotrophic Dictyochaceae which show marked points of contact with the Chrysomonadineae, the probably biflagellate, heterotrophic Ebriaceae (*Ebria*, fig. 185 E, *Hermesinum*) according to Hovasse (50a, 150) appear more nearly allied to Radiolaria and to certain of the Gymnodinioideae with an internal siliceous skeleton (p. 692), in whose neighbourhood this authority (151) would place them. The skeleton of Ebriaceae is more massive and intracellular throughout life. Zooxanthellae (cf. p. 658) are not uncommonly present (fig. 185 E, *a*).

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Class IV. BACILLARIOPHYCEAE

The Diatoms are unicellular, sometimes colonial forms which enjoy a very wide distribution in all kinds of habitats and play a very important rôle, especially in the aquatic vegetation of the world. The aquatic forms are a conspicuous feature both in freshwater and marine plankton (cf. p. 607), and in addition afford a host of epiphytes, while in the photic regions of salt and fresh waters alike they constitute one of the most important elements of the bottom-living flora. Everyone will be familiar with the brown scums and skins found on various kinds of substrata, as well as with the fluffy brown growths caused by abundant epiphytic Diatoms. Diatoms also often appear as brown or greenish films on damp mud, as on that of salt-marshes(21 *a*). Many Diatoms are very sensitive to changes in the salt-content of the water, and according to Kolbe(108) can be used as indicators of the degree of salinity. According to him this is the principal ecological factor determining the distribution of Diatoms. Other important factors are temperature and quantity of dissolved organic substance(33 *a*). A considerable number of forms occur in or on the soil, while extensive coverings of Diatoms have been recorded especially on sandstone surfaces (237).

The remarkable sculpturing of the silicified cell-walls renders Diatoms objects of great beauty and affords a fascinating study for those interested in minutiae, so that Diatoms have long been made the subject of special investigation by microscopists. This has had the disadvantage that too much stress has been laid on points of minute detail, while more important aspects have been neglected.

The Bacillariophyceae appear as a sharply circumscribed group of rather highly evolved forms which afford few points of vantage either for the tracing of their phylogeny or of their affinities with other groups of Algae. Pascher(164) has collected evidence indicating a relationship with Xanthophyceae and Chrysophyceae (cf. p. 642), and this is far more clearly founded than the older views relating Diatoms to Phaeophyceae or Conjugales which are really only of historical interest, since the resemblances to these groups are purely superficial.

The Chemistry of the Cell-wall

According to Mangin(122) the walls are composed of pectin impregnated throughout with silica, except for an outer often mucilaginous portion, found especially in plankton Diatoms, consisting of pectin only and frequently readily demonstrable by slight staining with aniline dyes. The silica can be extracted by the action of hydrofluoric acid[1] leaving the soft organic pectin membrane, or the pectin can be removed by calcination or maceration, leaving only the siliceous constituent; in either case all the markings of the intact cell can be recognised.

Liebisch (117, 118) has, however, shown that in many forms (and perhaps in all) there is no interpenetration of the two constituents and that the diverse parts of the diatom-membrane consist of an inner pectin-layer and an outer layer probably composed of hydrated silica ($SiO_2 + x\ H_2O$), similar to opal and without any admixture of organic material. The inner layer is closely adpressed to the outer and therefore shows the impressions of all the markings found on the siliceous shell (fig. 198 A, p. 594). In the coarser forms the pectin layer is often thicker than the siliceous one, while in thin-walled plankton Diatoms it may be very hard to recognise.

Richter (187, 188) came to the conclusion that the membrane contained sodium silicate combined with an organic compound, because he found that marine Diatoms must be supplied with sodium chloride and can utilise potassium silicate. Sodium has, however, not yet been shown to be essential for the growth of freshwater Diatoms, and it seems unlikely that the diatom-membrane which is so hard to dissolve should consist of one of the more readily soluble silicates (cf. (20) p. 353, (117) p. 241). According to Coupin (37) Diatoms can only employ aluminium silicates as the source of silica, but this requires confirmation. Brieger (20) finds that most Diatoms obtain their siliceous material from dissolved silica-compounds; only in the case of *Fragilaria elliptica* was the faculty of dissolving colloidal silica established.

The amount of silicification varies appreciably in different Diatoms, some like *Cylindrotheca* being so feebly silicified that weak hydrochloric acid is sufficient partly or entirely to dissolve the membrane. Under certain unknown cultural conditions, but in the presence of silica, certain Diatoms (marine forms of small size, *Nitzschia palea*) fail to produce the siliceous envelope; the species concerned are not necessarily those which are feebly silicified. In such cases no traces of the envelope remain on incineration (6). Bachrach and Lefèvre (4) found that such forms showed no decrease in vitality, multiplying actively and retaining more or less the normal shape. They exhibit movement like ordinary individuals and are stated also to conjugate with production of a rounded zygote[2] (5). Both Richter (187) and Geitler (57) have observed an escape of the protoplasts from the valves in cultures of marine Diatoms; the latter regards such phenomena as pathological.

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[1] Frenzel (42) was able to dissolve the siliceous component of the membrane of *Melosira* by prolonged treatment with steam.

[2] The figures, however, leave it doubtful whether copulation- or division-stages are involved.

The General Construction of the Diatom-cell

The diatom-cell (often spoken of as a *frustule*) has a wall composed of two, usually equal halves, the older (*epitheca*) fitting closely over the younger (*hypotheca*) (fig. 186 B, C, *e*, *h*). Each half consists of (*a*) a thin, commonly somewhat convex ***valve*** (*v*), the edges of which are more or less incurved and attached to (*b*) a ***connecting-band*** (*g*) in the form of a closed or probably often open hoop ((57) p. 74, (163)); it is the two connecting bands, together forming the *girdle*, that fit over one another. Thus, the individuals of the common genus *Pinnularia* (fig. 186 A–C) have the general form of an oblong box, whilst in such a Diatom as *Cyclotella* (fig. 186 F, G) the frustule may be likened to a circular pill-box. In either case the bottom and top of the box correspond to the two valves, the sides to the two overlapping connecting-bands.

It will be apparent, therefore, that the diatom-cell may be regarded from two aspects, viz. that in which one or other valve is seen (*valve-view*, fig. 186 A, G) and that in which the girdle is exposed to view (*girdle-view*, fig. 186 B, F); whilst the latter is very commonly rectangular in outline, the valve-view varies very much in shape in the different genera and species. The connecting-bands are able to grow in width ((92) p. 210, (140)), whereby the two valves become further removed from one another and the length of the cell increases, but the valves are not usually (cf. p. 616) capable of enlargement. When an appreciable part of the edge of the valve is bent over, this portion is of course visible on either side in the girdle-view; this may be called the *valve-jacket* ("Schalenmantel" of the Germans, cf. fig. 186 C, *j*). The valve may pass by a gradual curve into the valve-jacket or the two may be separated by a sharp angle. While the valves are usually ornamented in a characteristic manner, the connecting-bands (*girdle*) are commonly smooth.

The long axis of a diatom-cell is constituted by the line joining the centre-points of the two valves and is usually called the ***pervalvar axis*** (fig. 186 B–E, *pa*); the majority of Diatoms are thus considerably broader than they are long. The plane of cell-division, which lies at right angles to the pervalvar axis and is known as the ***valvar plane*** (fig. 186 B–E, *vp*), is strictly speaking never a plane of symmetry, since the one valve is always larger than the other; it is usual, however, to disregard this slight difference and to speak of asymmetry in the valvar plane only when the two valves are dissimilar also in other respects (*Achnanthes*, figs. 188 D, 195 A, B). In Diatoms with circular valves, such as *Cyclotella* (fig. 186 F, G) and *Coscinodiscus* (fig. 187 A) the valves are radially symmetrical about the pervalvar axis. These are known as Centric Diatoms (Centrales), but the Centrales[1] also

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[1] These also possess other characteristics, as will be apparent from the subsequent matter.

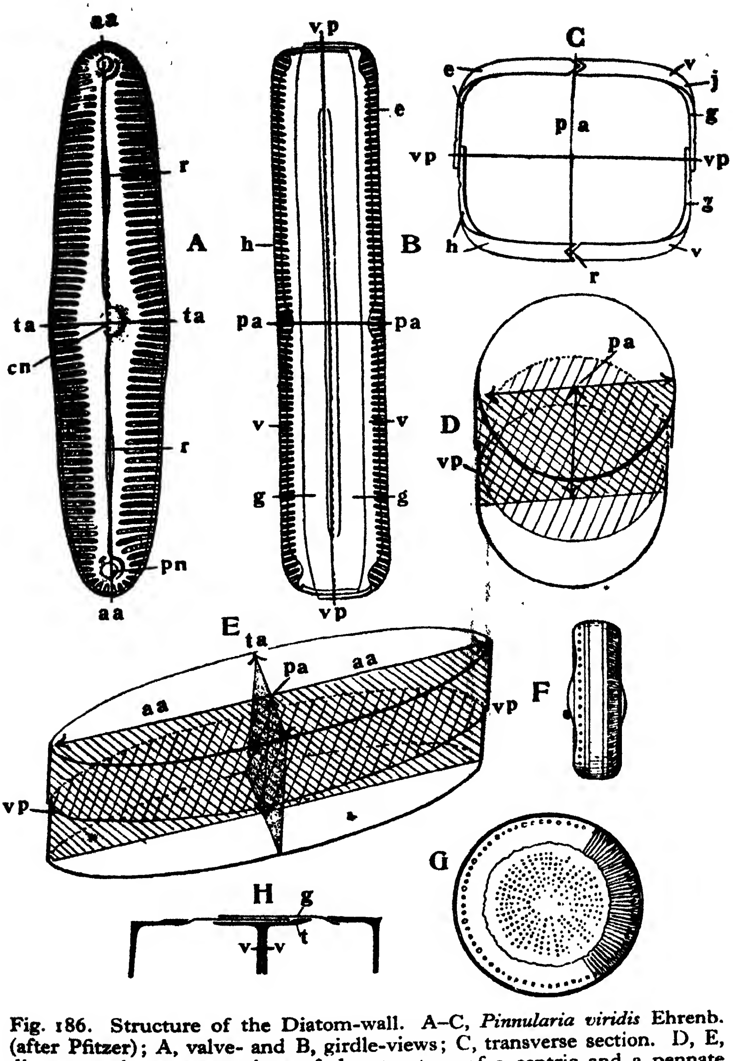

Fig. 186. Structure of the Diatom-wall. A–C, *Pinnularia viridis* Ehrenb. (after Pfitzer); A, valve- and B, girdle-views; C, transverse section. D, E, diagrammatic representations of the structure of a centric and a pennate diatom respectively (modified from Hustedt); transapical plane (in E) dotted, valvar plane cross-hatched, apical plane simple lines. F, G, *Cyclotella comta* (Ehrenb.) Kütz. var. *affinis* Grun. (after Van Heurck, from Karsten); F, girdle- and G, valve-views. H, *Eunotia didyma* Grun. var. *elegantula* Hustedt (after Hustedt), division-stage. *aa*, apical axis; *cn*, central nodule; *e*, epitheca; *g*, girdle; *h*, hypotheca; *j*, valve-jacket; *pa*, pervalvar axis; *pn*, polar nodule; *r*, raphe; *t*, junction of valve with girdle; *ta*, transapical axis; *v*, valve; *vp*, valvar plane.

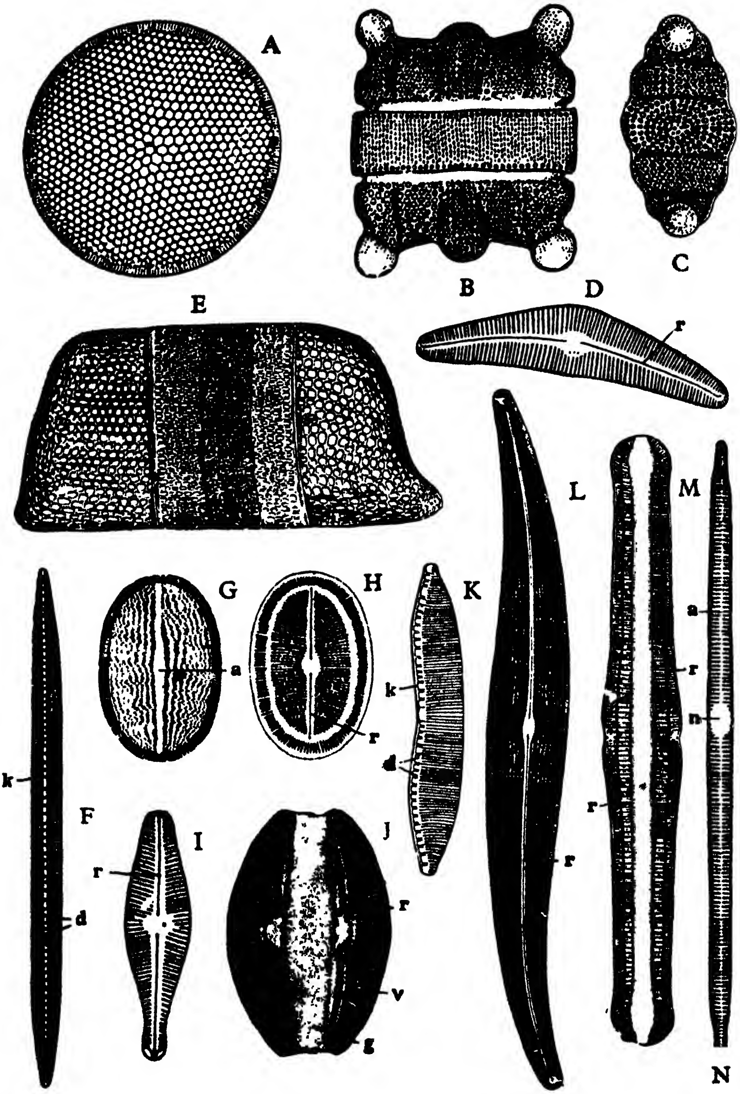

Fig. 187. Diverse forms of Diatoms. A, *Coscinodiscus excentricus* Ehrenb. B, C, *Biddulphia pulchella* Gray. D, *Cymbella cistula* (Hempr.) Grun. E, *Isthmia enervis* Ehrenb. F, *Bacillaria paradoxa* Gmel. G, H, *Cocconeis*

include forms in which the valves are triangular (*Triceratium*, fig. 193 D) or otherwise shaped and in which the number of planes of symmetry is consequently limited. Thus, in most species of *Biddulphia* (fig. 187 B, C) the valves are elliptical with only two planes of symmetry, while in *Isthmia* they are likewise elliptical but produced towards one side (fig. 187 E), so that there is only one plane of symmetry. Centric Diatoms are far more abundant in the sea than in freshwater, and the marine forms, moreover, attain a much larger size than the freshwater ones.

In forms like *Pinnularia* (fig. 186 A), with oblong cells, the valve is isobilateral with only two planes of symmetry, one about the axis joining the two poles of the valve (the *apical* or *sagittal* axis, *aa*), the other about the transverse axis of the valve (the *transapical axis*, *ta*) (cf. also fig. 186 E). The plane running through the apical and pervalvar axes and therefore passing through the poles of the respective valves is known as the *apical plane* (sagittal plane) (shaded with lines sloping down to the right in fig. 186 E), while that running through the transapical and pervalvar axes is known as the *transapical plane* (transversal plane) (dotted in fig. 186 E). The numerous Diatoms exhibiting this more limited symmetry are classed as Pennate Diatoms (Pennales), but they also include forms in which the valves possess only one plane of symmetry (either the apical plane, e.g. *Gomphonema*, fig. 187 I and *Licmophora*, fig. 190 F, or the transapical, e.g. *Cymbella*, fig. 187 D) and are therefore zygomorphic. In forms like *Cymbella*, which are asymmetric about the apical plane, the valves are usually described as dorsiventral.

Since the valve is usually the most characteristic part of the diatom-frustule, a brief consideration of some of its more outstanding features will help towards an initial comprehension of the group. In many cases the valves are ornamented with striae which, as a general rule, either readily or only with the help of the best optical equipment, resolve themselves into linear series of dots (cf. p. 577). The distribution of the striae and other markings constitutes the most obvious difference between Centric and Pennate Diatoms, especially when the valves of the former are not radially symmetrical. In Centrales the valves bear radially disposed striae or concentric markings (figs. 186 G, 187 A, C), while in Pennales they are arranged in two

placentula Ehrenb. var. *lineata* Van Heurck. I, *Gomphonema ventricosum* Greg. J, *Amphora ovalis* Kütz. K, *Hantzschia amphioxys* (Ehrenb.) Grun. L, *Gyrosigma attenuatum* (Kütz.) Rabenh. M, *Rhopalodia gibba* (Ehrenb.) O. Müll. N, *Synedra ulna* (Nitzsch.) Ehrenb. A, C, D, F–I, K, L, N, valve-views; G upper, H lower valve; the others girdle-views. *a*, axial area; *d*, carinal dots; *g*, girdle; *k*, keel; *n*, false central nodule; *r*, raphe; *v*, valve. (A, F, I, K after Hustedt; B, C, E after Smith; D after Skvortzow; the rest after Meister.)

series, one on either side of the apical axis (figs. 186 A, 187 D, I, N).

In pennate forms like *Synedra* (fig. 187 N) and *Fragilaria* (which belong to the so-called Araphideae)[1] the two systems of striae are separated by a narrow linear smooth area (*axial area*, *a*), devoid of markings and occupying the apical axis of the valve. This smooth area is often spoken of as a *pseudo-raphe*, since it simulates the true raphe found in this position in *Pinnularia* (fig. 186 A, *r*), *Gomphonema* (fig. 187 I, *r*), etc. In these latter genera (belonging to the Biraphideae)[1] the smooth axial area is commonly wider and shows a *central* and two *polar nodules* (fig. 186 A, *cn*, *pn*) which are internal thickenings of the wall; between the central and each polar nodule there extends a well-marked line (*r*), actually a longitudinal slit in the valve, and this constitutes the true *raphe* which will be dealt with more fully below (p. 583). Raphe and axial area are not uncommonly curved, as in *Gyrosigma* (fig. 187 L). In forms possessing merely a pseudo-raphe (Araphideae) the axial area may widen at the centre and sometimes also at the poles of the valves to form so-called false nodules (e.g. *Synedra*, fig. 187 N, *n*). In certain genera (e.g. *Cocconeis*, *Achnanthes*) one valve possesses a pseudo-raphe (figs. 187 G, *a*, 195 B), the other a true raphe with both central and polar nodules (figs. 187 H, *r*, 195 A). Such forms are grouped as Monoraphideae[1] in contrast to those possessing a raphe on both valves (*Pinnularia*, *Navicula*, etc.) which are classed as Biraphideae.[1] Centric Diatoms are altogether devoid of raphe or pseudo-raphe.

In all the genera just mentioned the valves are symmetrical about the apical axis, but in a number of the Biraphideae, as already noted, they are dorsiventral (145). Thus, in *Cymbella* (fig. 187 D) and *Amphora* (fig. 187 J) the valves, as well as the raphe, are more or less curved parallel to the apical axis and the raphe tends to lie nearer to the ventral (plane or concave) than the dorsal (convex) margin (cf. fig. 188 A). In both genera too the connecting bands are wider on the dorsal than on the ventral surface of the frustule (cf. fig. 188 A′), so that the valves are slightly tilted and one girdle is broader than the other. In *Amphora*, moreover, the valves are no longer plane, but shaped like a gable in transverse section (fig. 188 A′), that is to say they are crested, the valve-jacket being strongly developed. These features are responsible for the fact that individuals of this genus nearly always present their girdle-view to the observer (fig. 187 J). In *Rhopalodia* (Epithemioideae) (146, 149) much the same obtains, but the raphe is lodged in the crest of the gable (fig. 188 C′, *r*) and not along its sloping ventral surface as in *Amphora*, so that in the girdle-view the raphe is seen immediately adjacent to the dorsal edge of the valve-jacket (fig. 187 M, *r*).

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[1] Cf. pp. 640, 641.

A somewhat different type of valve-structure is found in the Nitzschioideae.[1] Here the valves are possessed of a more or less projecting keel (fig. 188 F′, *k*) which runs along their whole length (fig. 187 F, *k*), is marked with more or less evenly spaced (circular or oval) carinal dots (*d*, cf. p. 588) and contains a raphe in the form of a longitudinal canal with or without central and polar nodules. In

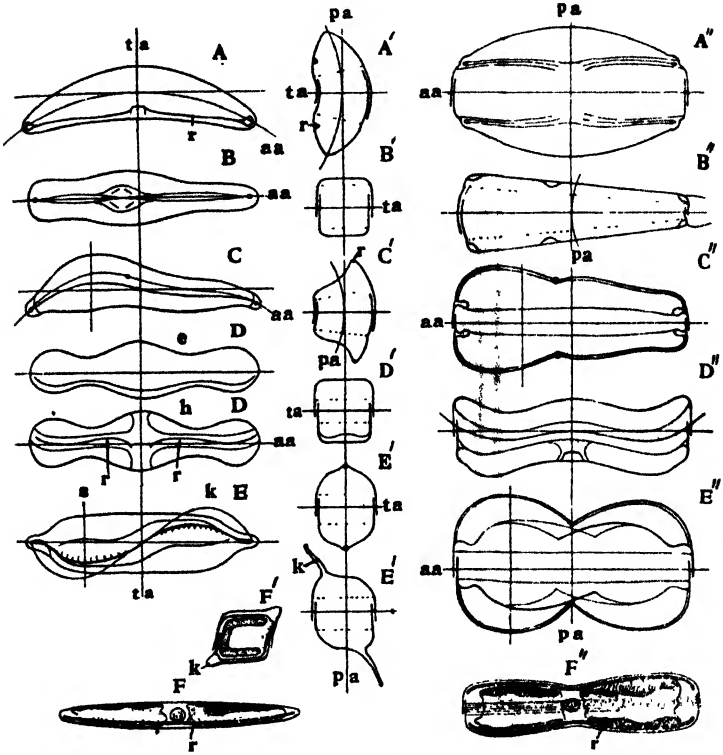

Fig. 188. Symmetry relations of various Diatoms (F′ after Pfitzer; F, F″ after Karsten; the rest after O. Müller). A, *Amphora ovalis* Kütz. B, *Gomphonema elegans* Grun. C, *Rhopalodia vermicularis* Müll. D, *Achnanthes inflata* Grun. E, *Amphiprora alata* Kütz. F, F″, *Nitzschia commutata* Grun.; F′, *N. palea* Kütz. A, B, C, etc., valve-views or sections through the valvar plane; A′, B′, C′, etc., sections of frustules through the transapical plane; A″, B″, C″, etc., girdle-views or sections through the apical plane; in D *e* is the epivalve, *h* the hypovalve; in E′ the lower figure is a section through the line *s* in E. *aa*, apical axis; *k*, keel; *pa*, pervalvar axis; *r*, raphe; *ta*, transapical axis.

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[1] Cf. p. 641.

Bacillaria (fig. 187 F) the keel is median, whilst in *Nitzschia* (fig. 188 F) it is often displaced towards one side of the valve and in *Hantzschia* (fig. 187 K) this is always the case. In *Nitzschia* the cross-section of the frustule (transapical plane) is usually rhomboidal, the two parts of the valve meeting at an acute angle in the keel (fig. 188 F'),

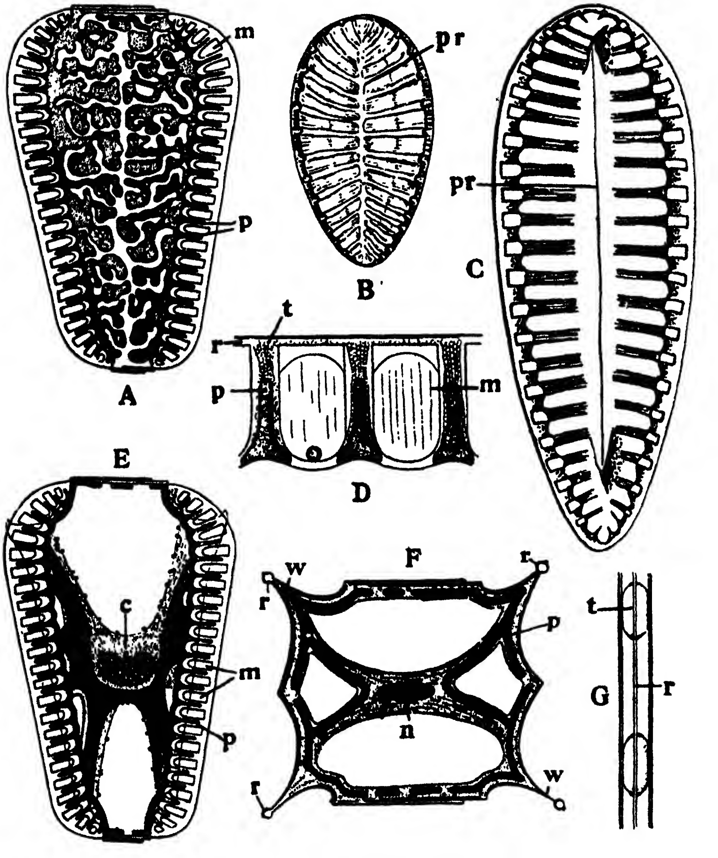

Fig. 189. Structure of *Surirella*. A, C–G, *S. Capronii* Bréb.; A, E, girdle-views, A from the surface showing the lobes of the chromatophores, E in optical section (apical plane); C, valve-view; D, part of a wing from the surface, showing the narrow canals separated by wide strips of membrane (*m*); F, transverse section (transapical plane); G, view of wing from outer edge. B, *S. striatula* Turp. *c*, centrosome; *m*, strips of membrane between canals in wing; *n*, nucleus; *p*, lobes of chromatophore; *pr*, pseudo-raphe; *r*, raphe; *t*, canal in wing communicating with raphe; *w*, wing. (B after Smith; C after Hustedt; the rest after Lauterborn.)

and the keels of the two valves are placed diagonally, so that the two sets of carinal dots do not lie on the same girdle-face. But in *Hantzschia*, which has dorsiventral valves (fig. 187·K), the cross-section of the frustule (transapical plane) is rectangular and the keels occupy adjacent angles, running in the ventral (concave) edges of the valves, so that both appear on the same girdle-face. In *Amphiprora* (Naviculoideae,[1] fig. 188 E) the valves are provided with a sigmoid keel (*k*) containing the raphe which is of the same type as in *Pinnularia*.

In the complex genus *Surirella* (Surirelloideae)[1] (115, 161, 179), lastly, the valve-view which is commonly elliptic or oval (fig. 189 B, C) shows a prominent median pseudo-raphe (*pr*) with a system of strong ribs on either side. The two margins of each valve are winged, as is very apparent in sections in the transapical plane (fig. 189 F, *w*), and the entire length of the somewhat dilated outer edge of each wing is occupied by a narrow slit-like canal (raphe, fig. 189 F, G, *r*) communicating with the external medium; each valve therefore possesses two raphes, but there are no nodules (cf. p. 588). The wings, as is usually plainly seen in the (often cuneate or subrectangular) girdle-view (fig. 189 A, E), contain a system of rather narrow transverse canals (*p*) through which the protoplasm of the cell communicates with that in the raphe (*r*), these canals being separated from one another by broad intervening strips of membrane (*m*) (cf. fig. 189 D).

INTERCALARY BANDS AND SEPTA

The relatively simple structure of the frustule described at the outset is complicated, especially in many Pennate Diatoms, by the interposition of intercalary bands (141) between the valves and their connecting-bands. These intercalary bands are really secondary connecting-bands and are usually well seen in the girdle-view (fig. 190 G, H, *i*). Like the connecting-bands they are probably in many cases open hoops. Often there is only one such intercalary band in each half of the frustule (*Denticula*, *Epithemia*), but in *Tabellaria* (fig. 190 H) there are from two to several, while in the marine *Rhabdonema* (fig. 190 A) as many as 28 intercalary bands may occur in each theca, the number being often unequal in epitheca and hypotheca.

In most cases the intercalary bands are produced internally into *septa* forming incomplete partitions running parallel to the valves. In *Tabellaria* (fig. 190 H, I, *s*) these septa do not reach to the centre of the frustule and successive septa arise from alternate poles of the intercalary bands, while in *Licmophora* (fig. 190 B, E) the septa extend from the broader pole of the cell for a varying distance towards the

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[1] Cf. p. 641.

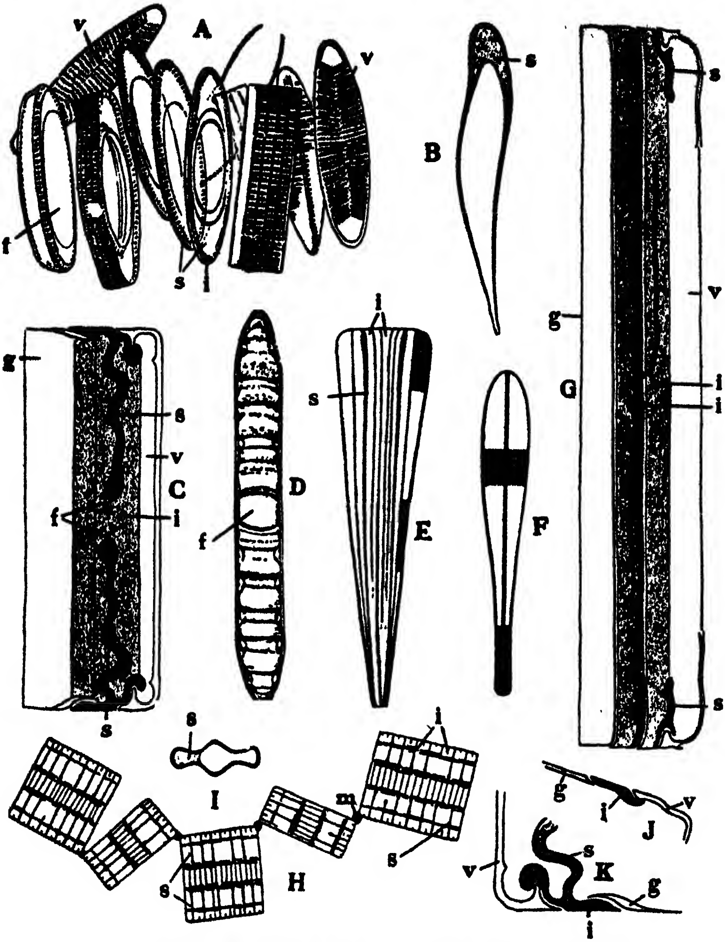

Fig. 190. Intercalary bands and septa. A, *Rhabdonema arcuatum* (Lyngb.) Kütz., frustule dissociated into its constituent parts. B, E, F, *Licmophora*; B, *L. lyngbyei* (Kütz.) Grun., intercalary band with septum; E, girdle- and F, valve-views of *L. gracilis* (Ehrenb.) Grun. C, K, *Grammatophora maxima* Grun.; C, half a frustule; K, corner of same. D, *G. serpentina* Ralfs, septum. G, *Rhabdonema adriaticum* Kütz., half a frustule. H, I, *Tabellaria flocculosa* (Roth) Kütz; H, colony; I, intercalary band with septum; J, *Climacosphenia moniligera* Ehrenb., corner of a frustule, showing connections between valve (*v*), intercalary band (*i*), and girdle-band (*g*). *f*, foramen; *g*, girdle-band; *i*, intercalary band; *m*, mucilage; *s*, septum; *v*, valve. (A, D after Smith; E, F after Grunow; H, I after West; the rest after O. Müller.)

centre. In many Pennales, however, the septa extend from all sides into the frustule. Those of *Rhabdonema* are commonly slightly curved (fig. 190 G, *s*), are marked with transverse ribs, and are perforated by from one (fig. 190 A) to three large apertures. In *Grammatophora* (fig. 190 C, D) they are markedly undulate, have a central foramen (*f*) and are very conspicuous in the girdle-view (fig. 190 C).

The single intercalary band in each half of the frustule of some species of *Epithemia* (fig. 191 B) and of *Climacosphenia* bears a septum perforated by a row of more or less rounded apertures (*f*). These, in *Epithemia*, lead into chambers between the septum and the valve which are cut off from one another by a system of further septa placed at right angles to the valve and appearing both in the valve- and girdle-views as prominent ribs (fig. 191 A, *s*). A very similar structure occurs in *Denticula* (fig. 191 F, G). *Mastogloia* (Naviculoideae, fig. 191 C, E) has in each half of the frustule a longitudinal septum (*s*) perforated by a large oval foramen (*f*) drawn out at the two poles, while the marginal part of the septum is divided into a row of variously shaped chambers (*c*); the partitions between these appear as strong transverse ribs in valve-view (fig. 191 C) and as a row of coarse markings along the edge of the valve in girdle-view (cf. fig. 191 D).

Among the Centrales intercalary bands are specially developed in the Solenoideae,[1] where their large number conditions an elongation of the pervalvar axis so that, unlike most Diatoms, the frustules are here much longer than they are broad. A typical instance is furnished by *Rhizosolenia* (fig. 191 H, M), where the cylindrical frustules have asymmetrical calyptra-like valves (*v*) terminating in an excentric spine or long seta, while the long intervening girdle is composed of numerous, usually scale-like intercalary bands (*i*) which are often more or less imbricate. In some of the allied marine forms (e.g. *Corethron*, fig. 203 A, *Dactyliosolen*) the intercalary bands are ring-shaped like those of the Pennales. Transverse septa are found in certain Biddulphiaceae (e.g. *Terpsinoë*, fig. 191 L) (139).

In all cases the connection between the valves and the connecting-bands, as well as between the valves and the intercalary bands when present, is a firm one. The edges are sometimes merely sharp and knife-like (figs. 186 H, 190 J), while in most cases there are special flanges (141) which serve to strengthen the junction (cf. *Grammatophora*, fig. 190 K).

While the above-discussed septa are regular features of the species possessing them, certain other internal structures are met with only occasionally and may at other times be completely lacking. The most familiar example is furnished by the craticular formations (118, 149),[2] often

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[1] Cf. p. 640.

[2] See (87), (111), (118), (149). A list to date of the Diatoms in which these structures have been observed is given by Liebisch ((118) p. 5).

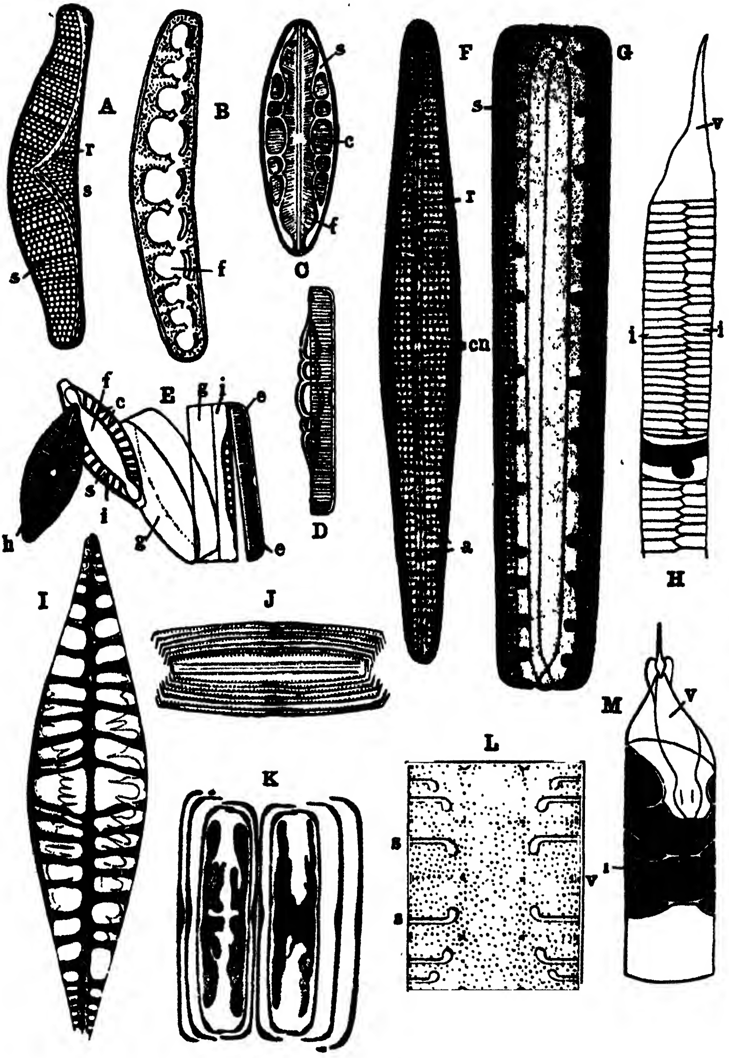

Fig. 191. A, *Epithemia argus* Kütz., valve-view. B, *E. alpestris* Grun., septum. C, D, *Mastogloia exigua* Lewis; C, valve-view with intercalary band; D, half frustule in girdle-view. E, *M. Smithii* Thw., frustule dissociated into its individual parts, the three parts of the epitheca on the right in girdle-view, those of the hypotheca on the left in valve-view. F, G, *Denticula*

met with in *Navicula cuspidata* (fig. 191 I). These are strongly silicified structures of the same shape as the valves and apposed to the inner surfaces of the latter; they are provided with a prominent median rib from which strong transverse ribs extend out towards the margin. Of an analogous nature are the internal valves,[1] commonly met with in *Meridion circulare*, in species of Naviculaceae (24, 48), *Nitzschia*, *Surirella* and in diverse species of *Eunotia*; in *E. serpentina* Hustedt (87) records as many as seven of these internal valves fitting the one within the other and differing from the true valve in the possession of different markings and the absence of the raphe (cf. also fig. 191 J, K). Similar structures are known also among Centrales (172). According to Liebisch ((118) p. 56) such internal valves are formed as a result of dilution or concentration of the medium combined with unfavourable nutritive conditions (cf. also (24), (177)); they have indeed often been recorded from waters of higher concentrations.

THE DETAILED STRUCTURE OF THE VALVE

The markings on the valves[2] are simplest in structure among the Pennales. The characteristic *striae* are, with good lenses, in the majority of cases resolved into linear series of small dots (*punctae*, figs. 187 J, 192 B) due to cavities (areolae) situated within more or less pronounced ridges of the wall which project either towards the inside or the outside. It is the close and regular arrangement of the punctae that causes them to appear as striae. They are so extremely fine and constant in arrangement in some species (e.g. *Amphipleura pellucida*, fig. 192 E) as to furnish excellent objects for testing the definition and angular aperture of microscope-lenses. All gradations exist from very fine striae to conspicuous ribs or *costae* (cf. fig. 187 D, I), but these latter are not always composed of series of punctae. In the large *Pinnularias* (147) they represent transversely distended chambers (fig. 192 A) within the inner part of the valve (*v*) communicating with the cell-cavity by oval foramina (*f*), whose edges appear as a pair of fine longitudinal lines running over the system of trans-

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[1] For literature, see footnote 2 on p. 575.

[2] See (148), (150–152), (214), (225). Muller (152) recommends treatment with hot sodium carbonate and potash in studying the structure of the valves.

Vanheurcki Brun; F, valve and G, girdle-views. H, *Rhizosolenia eriensis* H. L. Smith, part of frustule. I, *Navicula cuspidata* Kütz., craticular skeleton. J, *Nitzschia obtusa* W. Smith, girdle-view, internal valves. K, *Anomoeoneis pannonica* Grun., girdle-view, internal valves. L, *Terpsinoë musica* Ehrenb., girdle-view. M, *Rhizosolenia styliformis* Brightwell, half a frustule. *a*, carinal dots; *c*, chamber of septum; *cn*, central nodule; *e*, epitheca; *f*, foramen; *g*, girdle-band; *h*, hypotheca; *i*, intercalary bands (shaded in M); *r*, raphe; *s*, septum; *v*, valve. (A, F, G after Hustedt; B, I, M after O. Müller, C, D, J after Liebisch; E after Smith; H after Ostenfeld & Wesenberg-Lund; K after Geitler; L after Karsten.)

verse costae (fig. 192 F, *f*).[1] According to Köhler (107) the membrane overlying these costae is provided with numerous fine pores arranged along two series of intersecting lines.

In the majority of pennate forms the areolae are probably not open, although Köhler (107) states that definite pores are demonstrable in a number of cases. In the species of *Epithemia* ((148) p. 399) the rows of punctae occurring between the ribs (due to the transverse septa, p. 575) on the valves (fig. 191 A) are circular cavities widely open towards the interior of the cell (fig. 192 G, I, *a*); around the edge of the membrane covering in these chambers are a number of very fine, oblique pores (*p*) connecting the chamber with the outer surface. In *Pleurosigma* ((138) (148) p. 388, (151)) the wall of the valve is occupied by innumerable minute polygonal chambers (quadrangular in *Gyrosigma*, fig. 187 L), each opening towards the interior and exterior by a very narrow pore so that the wall possesses the structure of a minute sieve (fig. 192 H), the meshes of which are narrowed on the outer and inner sides. Perhaps similar minute perforations may yet be found in other Pennales. Many epiphytic and colonial members of this order show isolated, often rather large, pores which are usually situated near the ends of the valves and through which secretion of mucilage takes place (fig. 192 C, D, *p*).

Among the Centrales a relatively simple structure of the wall is found in *Melosira* (fig. 193 A), where it is traversed by numerous fine pore-canals forming a dense network and believed to be open both on the inner and outer sides[2] (143). In *Triceratium plano-concavum* (fig. 193 E, H), according to Hustedt (80), the areolae (*a*) constitute warts on the outer surface which are perforated by three slightly oblique pores (*p*), which converge and unite to form a single canal traversing the inner part of the wall (fig. 193 C, H). In most Centric Diatoms that have been examined, however, the valve bears internal or external ridges which form a network circumscribing the areolae. The latter thus appear as cavities which are either open towards the exterior (*Triceratium favus*, fig. 193 I, *Eupodiscus argus*) or towards the interior (*Coscinodiscus*, *Craspedodiscus*, *Isthmia nervosa*, fig. 193 B), while the membrane covering the chamber on the inner or outer side, as the case may be, is traversed by fine pores or by so-called *poroids* (*p*), the latter believed to be closed by a delicate membrane ((148) p. 396, (150) p. 424).

Thus, in *Coscinodiscus asteromphalus* (fig. 193 K) the primary wall bears a polygonal network, the meshes of which open to the interior

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[1] Transverse costae of another kind are seen on the valves of many forms provided with the above-mentioned transverse septa (*Meridion*, *Diatoma*, *Denticula*, etc.).

[2] With reference to the occasional dimorphism of the individuals in the colonies of *Melosira* (coarsely and finely punctate individuals, etc.) see (154).

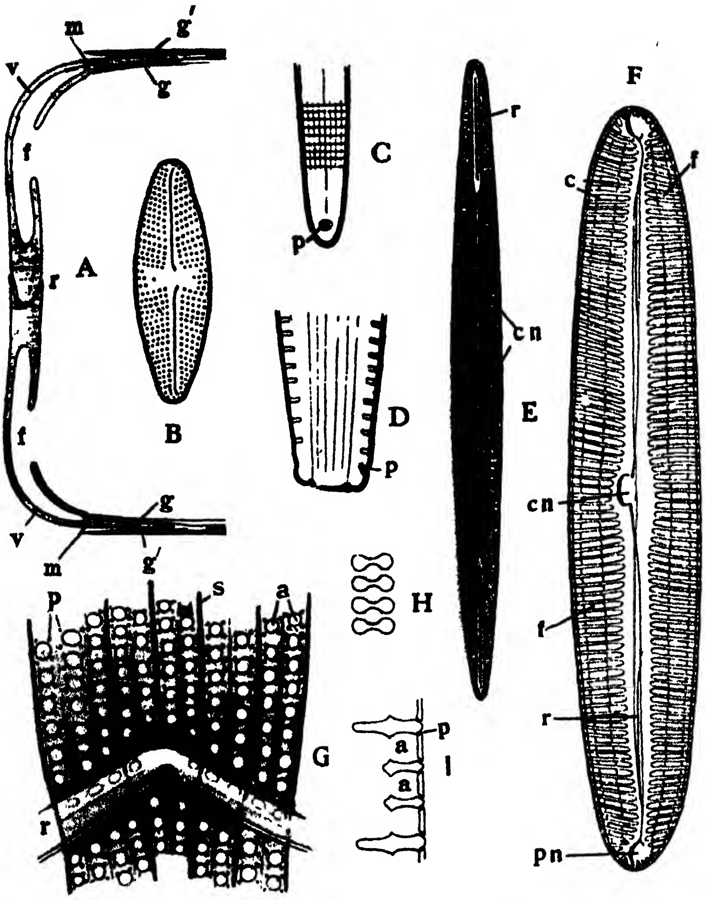

Fig. 192. Structure of the valve in Pennales. A, *Pinnularia*, diagrammatic representation of transverse section of hypovalve with parts of adjacent girdle-bands. B, *Navicula mutica* Kütz., valve-view. C, *Licmophora Jürgensii* Ag. and D, *L. Ehrenbergii* (Kütz.) Grun., showing mucilage-pores (*p*). E, *Amphipleura pellucida* Kütz., valve-view. F, *Pinnularia viridis* (Nitzsch) Ehrenb., valve-view. G, I, *Epithemia Hyndmanni* W. Sm.; G, part of valve-jacket with raphe (*r*), central nodule, areolae (*a*) and pores (*p*); I, section through three areolae. H, *Pleurosigma balticum* (Ehrenb.) Sm., section of cell-membrane. *a*, areolae; *c*, costae; *cn*, central nodule; *f*, foramen; *g*, *g'*, girdle; *m*, wall of valve; *p*, pores; *pn*, polar nodule; *r*, raphe; *s*, septum; *v*, valve. (B, E, F after Hustedt; the rest after O. Müller.)

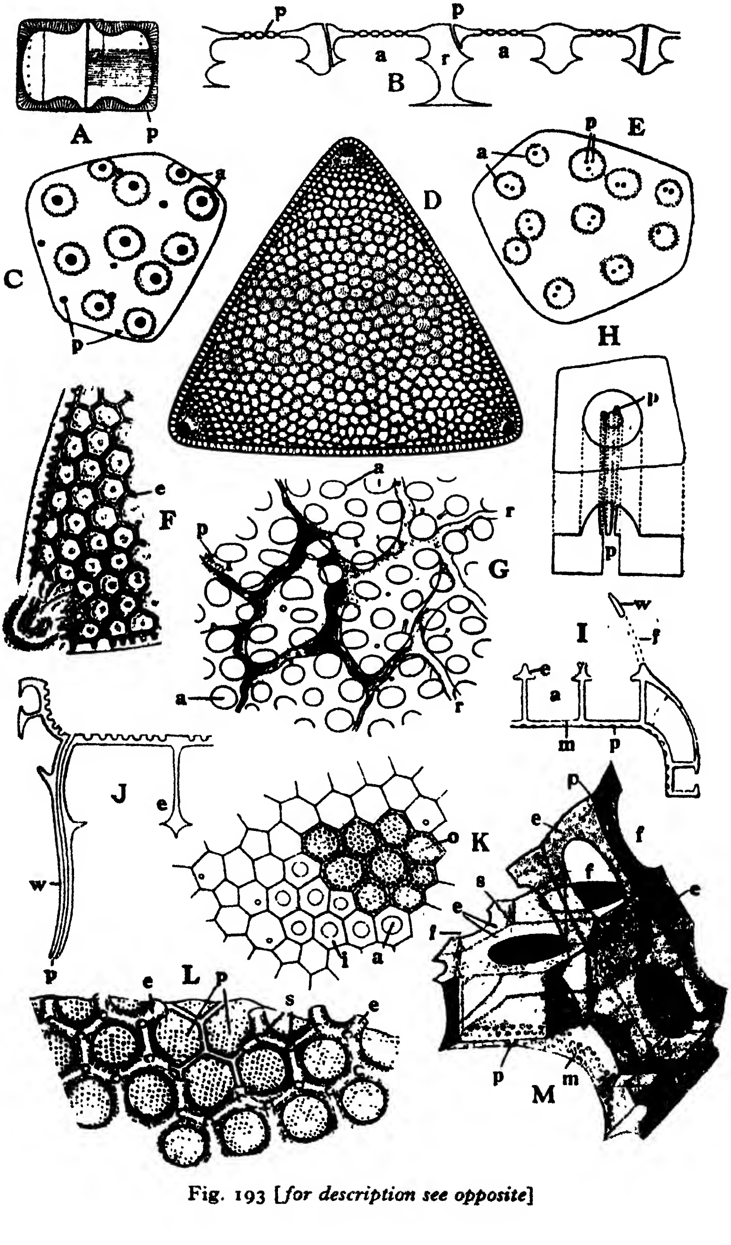

Fig. 193 [*for description see opposite*]

by wide circular apertures (*a*), while the covering membrane (*i*) is occupied by numerous poroids (*o*), some of which are believed to be actual pores (21, 150). In *Isthmia nervosa* (fig. 193 B, G) the chambers are shallow (148), being formed by short ridges projecting internally; occasional ridges extend deeper and form the coarse network (fig. 193 G, *r*) visible at a low focus, each mesh of which includes a number of areolae (*a*). The membrane covering each chamber bears at its periphery delicate, radially disposed ridges, while the central part is occupied by minute poroids (fig. 193 B, *p*). Occasional pore-canals, both here and in *Coscinodiscus*, traverse the ridges (fig. 193 B).

The primary membrane of *Triceratium favus* (138, 150) bears a network of external ridges (fig. 193 F, L, *e*) enclosing regular polygonal chambers and slightly broadened at their outer margins which circumscribe the rounded external apertures (fig. 193 I, *e*). The internal wall of each chamber is traversed by numerous poroids (*p*), some of which are believed to be true pores. At the edges of the valves the ridges are prolonged into wings (fig. 193 I, J, M, *w*) which are traversed by long pore-canals (*p*).

The examples here described should suffice to illustrate the complexity of structure of the diatom-membrane, the details of which are known only in relatively few cases. Since the rather thick siliceous envelope of the cells shuts off the contained protoplast from the environment, the presence of numerous thin areas, admitting of gaseous diffusion and an osmotic exchange, or even of direct apertures communicating with the exterior, is manifestly a necessity. Among the Pennales, where the large majority of forms are possessed of a direct connection between the protoplast and the exterior by way of the raphe, this may well suffice,[1] although it has been mentioned that direct perforation of the membrane is probable in *Pleurosigma* and other forms, while cavities in which the protoplast is separated only

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[1] In the Araphideae (cf. p. 640), which lack a raphe, no detailed study of the valve-structure appears yet to have been made.

Fig. 193. Structure of the valve in Centrales. A, *Melosira undulata* (Ehrenb.) Kütz., girdle-view. B, G, *Isthmia nervosa* Kütz.; B, section of membrane; G, inner surface of part of valve. C, E, H, *Triceratium plano-concavum* Brun; C and E, parts of membrane at a low and high focus respectively; H, diagram explaining structure of areolae, above from the surface, below in section. D, *T. distinctum* Janisch, valve-view. F, I, J, L, M, *T. favus* Ehrenb.; F, edge of valve, surface-view; I, J, sections of edge of valve, passing through edge of wing and foramen respectively (J inverted); L, enlarged surface-view, in part without the projecting edges over the foramina; M, diagram of structure of membrane at edge of valve. K, *Coscinodiscus asteromphalus* Ehrenb., membrane in surface-view, partly showing the outer (*o*) and partly the inner (*i*) surface. *a*, areolae; *e*, external enlargement of ridge; *f*, foramen; *m*, wall of valve; *p*, pores or poroids; *r*, ridges of membrane; *s*, outgrowths on surface of membrane; *w*, wing. (C, E, H after Hustedt; D after Schmidt; the rest after O. Müller.)

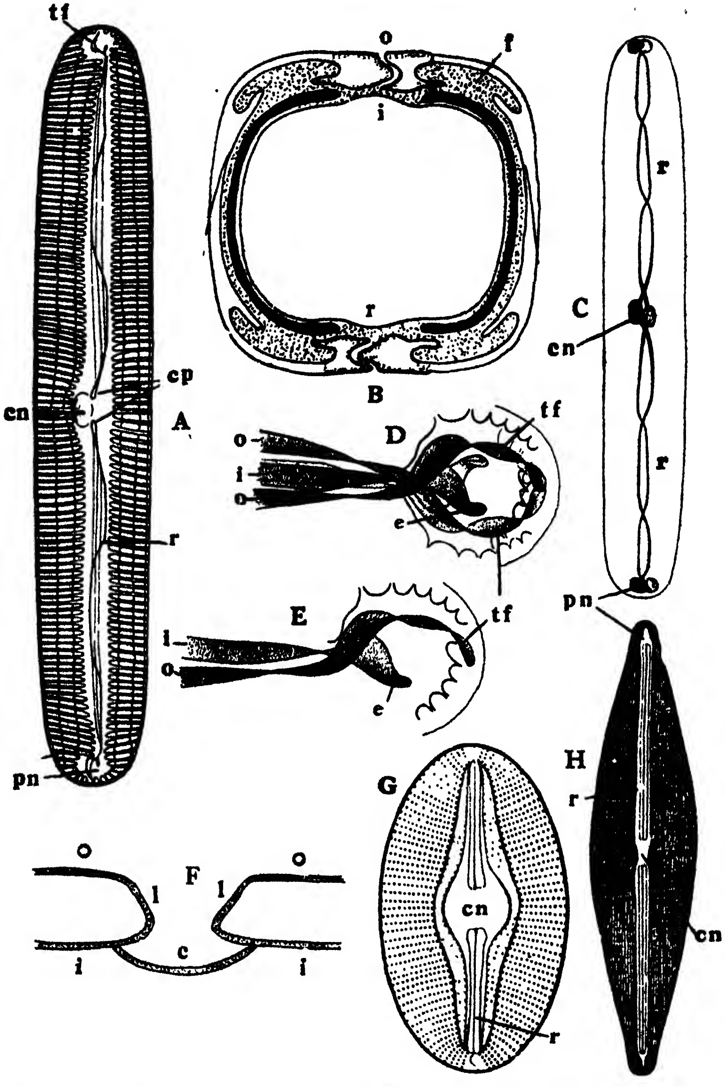

Fig. 194. Raphe-structure in Naviculaceae. A, *Pinnularia streptoraphe* Cl., valve-view. B–F, *P. viridis* Kütz.; B, transverse section of frustule, protoplast dotted, chromatophores black; C, diagrammatic surface-view of the two valves, showing the relative positions of the two raphes; D, polar nodules of the two overlying valves; E, single polar nodule showing terminations of

by a thin membrane from the outside medium exist in *Epithemia* and *Pinnularia*. In the Centrales, however, where a raphe is lacking, pores are probably imperative. Where actual apertures occur in the membrane they may not exceed a maximum diameter determined by the turgor-pressure of the cell-contents, since if the latter were greater than the resistance to flow through the aperture the protoplasm would escape. This statement is made on the assumption that the apertures occur also in the internal pectin-membrane. It is perhaps more probable, however, that the latter is not perforated, in which case it would constitute a firm boundary to the protoplast and the size of the apertures would be immaterial. The minimum diameter of the pores in the diatom-envelope is not of such an order as to interfere in any way with a free diffusion between the cell-contents and the external medium.

THE RAPHE

The raphe, met with in all Pennales except the Fragilarioideae (Araphideae),[1] is almost invariably associated with the power of spontaneous movement. It is encountered in a large proportion of the bottom-living forms. Its structure may be considered in the first place in one of the larger *Pinnularias* (Naviculoideae) where many of the details can be recognised without too much difficulty ((115) p. 10, (142), (144) (1896)). The two polar nodules (fig. 194 A, *pn*), appearing as highly refractive structures in the valve-view, are connected by the line of the raphe (*r*) which is interrupted at the central nodule (*cn*). A transverse section of the valve (fig. 194 B) shows the raphe (*r*) to be a V-shaped cleft opening towards the outside (*o*) and the inside (*i*), but narrowed down markedly at the apex of the V and possibly actually closed here by a lamella. In other words the valve between polar and central nodules is divided into two halves by a narrow slit, the plane of which runs obliquely through the substance of the valve and at some point, perhaps interrupted, curves back more or less sharply upon itself. In some of the more complex forms the raphe may appear variously undulated in a cross-section through the valve,

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[1] See p. 640.

the two parts of the raphe; F, structure of raphe at central nodule in a section through the apical plane. G, *Diploneis ovalis* (Hilse) Cl., valve-view. H, *Frustulia rhomboides* (Ehrenb.) De Toni var. *saxonica* (Rabh.) De Toni, valve-view. *c*, canal joining the two parts of the raphe at the central nodule; *cn*, central nodule; *cp*, central pores; *e*, enlarged end of inner fissure of raphe; *f*, foramen; *i*, internal and *o*, external fissures of raphe; *l*, canal connecting external and internal fissures in the central nodule; *pn*, polar nodule; *r*, raphe; *tf*, terminal fissure. (B after Lauterborn; C–F after O. Müller; the rest after Hustedt.)

whilst in others it is a straight slit ((142) p. 170). Its course in the apical direction in valve-view is rarely quite straight (fig. 194 C). In a surface-view of the valve the external fissure of the raphe appears as a distinct slit, whilst when it is markedly undulate along the pervalvar axis the points of bending appear as fainter lines alongside of the main slit (fig. 194 A).

At the central nodule (fig. 194 F), which is a solid internal thickening of the wall, the two overlying (external and internal, *o*, *i*) fissures of the raphe approaching from either pole are connected by a loop-like, somewhat sinuous canal (*l*). The points at which the external fissures dip inwards appear in the valve-view as a pair of *central pores* (fig. 194 A, *cp*) which are usually located a little towards one side of the apical axis. Within the inner part of the central nodule the two loops are connected by a horizontal furrow which is in communication with the protoplasm (fig. 194 F, *c*). The polar nodules are hollow enlargements of the wall projecting slightly towards the exterior (fig. 194 E), and within their outer wall the outer fissure (*o*) of the raphe terminates as a semilunar, slightly twisted slit (*tf*), the *terminal fissure*. This is readily recognisable in the valve-view (fig. 194 A, *tf*) and usually, though not always, these terminal fissures curve in the same direction at the two ends of the valve, though they always curve in opposite directions in the two valves of a frustule (fig. 194 D). The inner slit of the raphe, within the inner wall of the polar nodule (fig. 194 E), enlarges into a funnel-shaped structure (*e*) which is actually a fold of the membrane and projects into the apical protoplasm like a propeller. These funnels, like the terminal fissures, are curved in opposite directions in the two overlying polar nodules of a frustule, so that the two systems are complementary to one another (fig. 194 D).

It is not at present known whether this complex structure of the nodules is found in other Naviculoideae, but Hustedt ((87) p. 50) is of the opinion that a large number of these possess solid polar nodules and that hollow ones are only found in the advanced types. He also considers it probable that in some Naviculoideae the two parts of the raphe may be unconnected at the often ill-defined central nodules (as in *Eunotia*, cf. p. 585). Various members of this suborder show special modifications of the raphe-system. In *Stauroneis* the central nodule extends as a so-called *stauros* devoid of striae over the whole width of the valve. In *Frustulia* (*Vanheurckia*), regarded by many only as a section of the genus *Navicula*, both polar and central nodules are elongated in the apical direction and enclosed, along with the raphe, between two parallel siliceous ribs (fig. 194 H). In the section *Diploneis* of *Navicula* the central nodule is more or less square or rounded and prolonged at either end into pairs of processes enclosing the raphe (fig. 194 G). The central nodule in *Amphipleura* (fig. 192 E) is greatly elongated and appears as a narrow rib separating the two short portions of the raphe (*r*) which are enclosed between two parallel ribs uniting at each extremity of the valve to form the polar nodules.

We owe to Hustedt the elucidation of what may perhaps be regarded as the beginnings of the raphe among the Eunotiaceae (Raphidioideae). In *Peronia* (59) it appears only on one valve as two short slits, extending from the barely indicated, solid polar nodules for a short distance towards the centre of the valve and without any trace of a central nodule (fig. 195 K, *r*). Hustedt therefore concludes that the fissure is to be regarded as the primary part of the raphe-system of the Naviculoideae and that the nodules are secondary developments; Gemeinhardt, however, looks upon the raphe of *Peronia* as reduced.

A rather more advanced type among Eunotiaceae is found in *Eunotia* itself (78). The rectangular frustules of this Diatom are sometimes united by their valve-faces to form long, flexuous, ribbon-like filaments (section *Himantidium*), but in other species are solitary or more rarely occur as epiphytic clusters (*E. lunaris*). The valves are dorsiventral and arcuate or bow-shaped, often with an undulated dorsal margin (fig. 195 C). Near the poles are comma-shaped slits (*r*) each of which represents a rudimentary raphe perforating the ventral valve-jacket and extending for a short distance (at the most for a quarter of the length of the valve) on to the valve-face (fig. 195 D, E). This raphe consists of an outer (*o*) and an inner (*i*) fissure which are not superposed, but run at an angle to one another and are connected at each end by canals. Polar nodules in the shape of solid internal thickenings of the membrane are always recognisable (fig. 195 D, E, *pn*), while in some cases a slight thickening at each central pore (*cp*) indicates what Hustedt regards as the beginnings of a central nodule, of which therefore there are two on each valve. The two raphes of each valve form quite unconnected systems. Nevertheless, as Geitler (57) has recently shown, the species of *Eunotia* possess the capacity for movement, although the raphe perhaps in the main serves for the exchange of material with the environment.

From such a raphe-system as that seen in *Eunotia* the type found in the Naviculoideae could originate by the combination of both raphes of a valve into a common system. This could be accomplished by elongation of the two raphes until the two central nodules fused or by elongation of the latter until they came into contact ((78), (87) p. 50). In the latter connection the Naviculoideae with an elongate central nodule (*Amphipleura*, *Frustulia*) may indicate the direction of development. The Achnanthaceae (Monoraphideae), with *Achnanthes* (fig. 195 A, B) and *Cocconeis* (fig. 187 G, H), are characterised by an abortion of the raphe on one valve, probably in relation to their epiphytic habit.

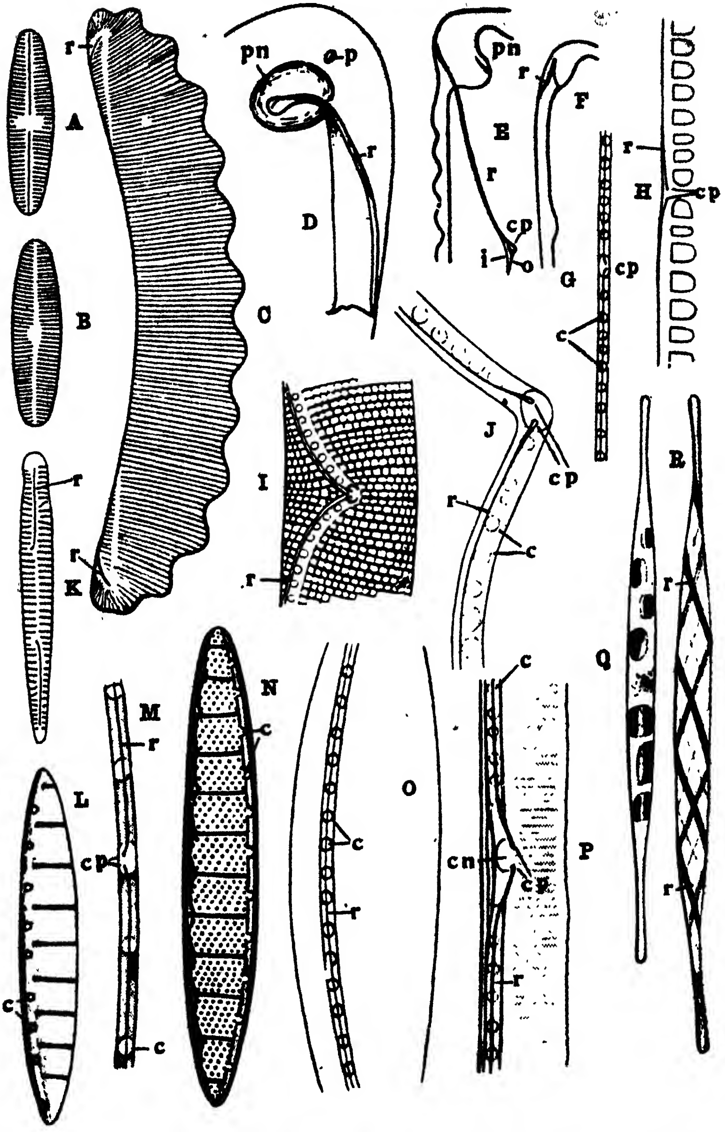

Fig. 195. A, B, *Achnanthes linearis* W. Sm., the two valves. C, *Eunotia robusta* Ralfs, valve-view. D, *E. americana* Kain et Schultze, end of valve. E, F, *E. epithemioides* Hust., ends of valves in girdle- (E) and valve-view (F).

The rather different type of raphe found in Nitzschioideae and Surirelloideae is connected with that of the Naviculoideae by way of the Epithemioideae, to which Hustedt (81) reckons *Denticula*, *Epithemia*, and *Rhopalòdia*. The common characteristic, which distinguishes Epithemioideae and Nitzschioideae from the Naviculoideae, is the possession of a raphe having the form of a cylindrical canal extending longitudinally through the membrane of the valve (cf. fig. 195 O, *r*) and communicating with the exterior by a narrow oblique fissure ((144) (1896), p. 56). This *canal-raphe* is typically without nodules and is usually located in a more or less marked crest or keel which either occupies the apical axis or lies excentrically towards one margin of the valve (cf. p. 571). Connection with the internal protoplasm is established by means of a row of rounded apertures or pits in the inner wall of the canal (cf. fig. 195 J, M, O, *c*) occurring at irregular intervals and occupying the whole width of the raphe. In those forms in which the canal-raphe occupies a prominent keel these apertures become lengthened into canals separated by strips of membrane. The external fissure of the canal-raphe is regarded as the equivalent of the outer fissure of the naviculoid raphe, while the pores correspond to the inner fissure of the latter.

Among the Epithemioideae (81) the raphe always consists of two separate branches terminating in more or less distinct central pores situated close together (fig. 195 I, J; cf. also fig. 191 F, *r*). Beneath these lies an elliptical area, similar to the rounded apertures seen beneath the rest of the raphe, but about twice as large and probably representing a fusion of two of them. In *Epithemia* (fig. 195 I, J) the canal-raphe is typically V-shaped in valve-view, the inconspicuous central pores lying in the middle of the valve or nearer to its dorsal margin, while the two branches of the raphe curve rapidly towards the ventral margin which they follow for the greater part of their course (cf. also fig. 191 A). In *Denticula* the raphe is raised on a slight keel, in some species occupying the apical axis, in others (*D. valida*, fig. 195 L–N) shifted almost to the margin of the valve. In *Rhopalodia* (fig. 187 M) the raphe lies in a keel which occupies the extreme edge of the frustule in the girdle-view (cf. p. 570).

G, H, *Nitzschia Tryblionella* Hantzsch, middle part of keel seen from the surface (G) and from the edge (H). I, J, *Epithemia argus* Kütz.; I, middle part of valve; J, central part of raphe enlarged. K, *Peronia erinacea* Bréb. et Arn., valve-view. L–N, *Denticula valida* (Ped.) Grun.; L, valve slightly on edge showing keel; M, the latter enlarged; N, valve-view. O, *Nitzschia granulata* Grun., middle part of valve tilted to show keel. P, *Hantzschia amphioxys* (Ehrenb.) Grun., middle part of valve. Q, R, *Cylindrotheca gracilis* (Bréb.) Grun.; Q, with chromatophores; R, empty valve. *c*, carinal pores; *cn*, central nodule; *cp*, central pores; *i*, inner and *o*, outer part of raphe; *p*, mucilage-pore; *pn*, polar nodules; *r*, raphe. (All after Hustedt.)

Among the *Nitzschias* (84) there are also forms showing central pores with a large underlying elliptical aperture (e.g. *N. longissima*, *N. Tryblionella*, fig. 195 G, H), but the pores are usually very close together; between them a faint central nodule can be distinguished, while the polar nodules though very small are distinct. The excentric keel which harbours the raphe is distinctly constricted in the region of the central nodule (fig. 195 H). There are, however, many *Nitzschias* (*N. scalaris*, *N. sigma*, etc., cf. fig. 195 O) in which the slit of the raphe can be followed without interruption from one end of the valve to the other and in which central pores are lacking. In *Hantzschia* (82) the raphe does not run in the keel, but lies in the ventral valve-jacket (fig. 195 P); from the closely adjoining central pores (*cp*) the two branches of the raphe rapidly approach the keel and run parallel with it, but shortly before they reach the poles they bend over on to the valve-edge and end in minute terminal pores.

The *carinal dots* of the Nitzschioideae are probably in some cases the actual apertures on the inner surface of the canal-raphe, in other cases the intervening strips of membrane ((82) p. 161), according as the latter are wider or narrower than the diameter of the apertures. The researches of Hustedt indicate that the canal-raphe at first (Epithemioideae) exhibits many of the essential features of the raphe of the Naviculoideae, but that among the *Nitzschias* reduction of the nodules with their complicated system of pores has taken place. It is not impossible, however, that from its first beginnings the raphe differentiated in two different directions, on the one hand following the line of development seen in Nitzschioideae and Surirelloideae, on the other resulting in the complex type found in the *Pinnularias*.

The rare Diatom *Cylindrotheca* (83) appears to be a member of Nitzschioideae which is strongly twisted about the apical axis. The cells are cylindrical with produced apices (fig. 195 Q, R), the main body showing a number of spiral lines, two of which are punctate (*r*) and are believed to harbour the canal-raphe, the punctae being the carinal dots.

In the *Surirellas*, as already mentioned, each edge of the valve, where it passes into the valve-jacket, is produced into a wing (fig. 196 A, *w*), the somewhat widened outer portion of which is occupied by a canal-raphe (*r*) communicating by a narrow fissure with the external medium. The two wings of a valve in most species extend to the poles where they are separated by a slight constriction and where the canal-raphe is probably in most cases interrupted, although in some it may run continuously over the poles. In some species one can distinguish distinct terminal pores, although these are sometimes only to be seen at one pole (fig. 196 D, E, *po*). Hustedt (85) has, moreover, shown that in certain species of the genus (*S. Neumeyeri*) the canal-raphe possesses distinct central pores at a point where, as in the *Nitzschias* above mentioned, the valve-margin is markedly constricted (fig. 196 C, right, *cp*). From these central pores the raphe passes on to the crest of the feebly developed wing and, after reaching the poles, extends over them and down the other wing until the two branches of the raphe meet, the terminal pores being in contact (fig. 196 C, left, *tp*). In *S. Baldjickii* not only central pores, but also the terminal pores on the other wing are clearly distinguishable, although both sets appear quite alike (fig. 196 B).

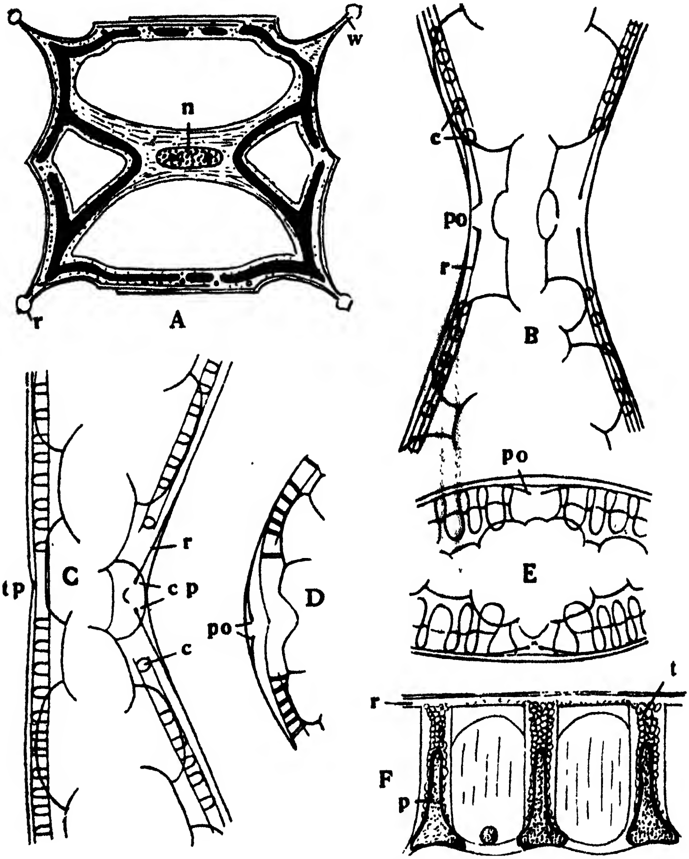

Fig. 196. Structure of the raphe in *Surirella*. A, F, *S. Capronii* Bréb.; A, transverse section of frustule, chromatophores black; F, wing from surface, enlarged. B, *S. Baldjickii* Norm., middle part of valve. C, *S. Neumeyeri* Jan., middle part of valves, on the left with terminal pores (*tp*), on the right with central pores (*cp*). D, *S. multicostata* Castr., basal pole of a valve. E, *S. colombonensis* Leud.-Fort., apical poles of a valve. *c*, internal apertures of canal-raphe; *n*, nucleus; *p*, process of chromatophore; *po*, terminal pores (in B, D, E); *r*, raphe; *t*, canal in wing communicating with raphe; *w*, wing. (A, F after Lauterborn; the rest after Hustedt.)

Hustedt is of the opinion that the raphe in *Surirella* is not actually double, but that it has become prolonged over the whole wing-like margin of the valve, ultimately with the complete elimination of the terminal pores by the fusion of the two branches. Further, in the majority of the species, the point of interruption of the raphe has been shifted from the middle of the valves to the poles of the apical axis. On this view the apical axis of most *Surirellas* is morphologically equivalent to the transapical axis of *S. Neumeyeri*, *S. Baldjickii* and the Nitzschioideae.

The valve-faces of *Surirella* are transversely folded like corrugated iron and the folds which appear as costae (fig. 189 B, C) are continued on to the wings and here harbour elongate canals. These communicate on the one hand with the canal-raphe and on the other with the main protoplast, in many cases even containing small lobes of the chromatophores (fig. 196 F, *p*). These canals are the equivalents of the apertures in the inner wall of the raphe of a *Nitzschia*, *Denticula*, etc. In the marine *Surirellas* these canals are more numerous than in the freshwater species and show no relation to the folds.

THE MOVEMENTS OF DIATOMS

Only those Diatoms that possess a raphe are capable of movement,[1] and apparently the canal-raphe, especially when located on a keel or wing, is more efficient than the type found in the Naviculoideae, since forms with such a raphe exhibit a greater capacity for movement ((85) p. 109). The motion is occasionally creeping and steady, more frequently jerky, and sometimes, but not necessarily, takes place along some kind of substratum. Some forms (e.g. *Amphipleura*) exhibit very slow movements. In *Surirella* the individuals show a peculiar rolling motion. In the planktonic *Bacillaria paradoxa* (fig. 200 G, H), in which the cells are united to form ribbon-shaped colonies, the frustules exhibit a highly characteristic gliding movement over one another. These movements of *Bacillaria* are autonomic, but according to Funk (44, 45) the colonies are mainly drawn out in the day and mainly contracted at night. Mechanical stimulation of a colony in the day-condition leads to approximation of the individuals, the degree of response depending on the strength of the stimulus and the temperature. Diatoms exhibit marked positive phototaxis (185).

In spite of much research (69, 114, 115, 142, 144) the mechanism of the movements remains unclear. It is highly probable that the raphe is in all cases occupied by streaming cytoplasm (27) in direct contact with the external medium and that the resulting friction is the cause of the

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[1] Siddall (219), however, records movement of a *Coscinodiscus* by means of delicate "pseudopodial" filaments. It is not clear from his account on what grounds these filaments are regarded as being cytoplasmic in nature and it is possible that they are mucilaginous.

movement. In the Naviculoideae, where the mechanism has been mainly studied, the cytoplasmic currents are in the same direction in the two parts of the raphe of a valve, viz. from terminal fissure to central nodule and again from central nodule to the other terminal fissure, whilst in the inner fissures of the raphe the current is in the opposite sense ((142) p. 178, (144) (1893)). The high osmotic pressure in the cells (calculated by Müller at 4–5 atmospheres) is sufficient to drive the cytoplasm into the complex system of canals in the nodules, whilst the twisted form of the terminal fissures must give a torsion to the cytoplasmic stream issuing from them.

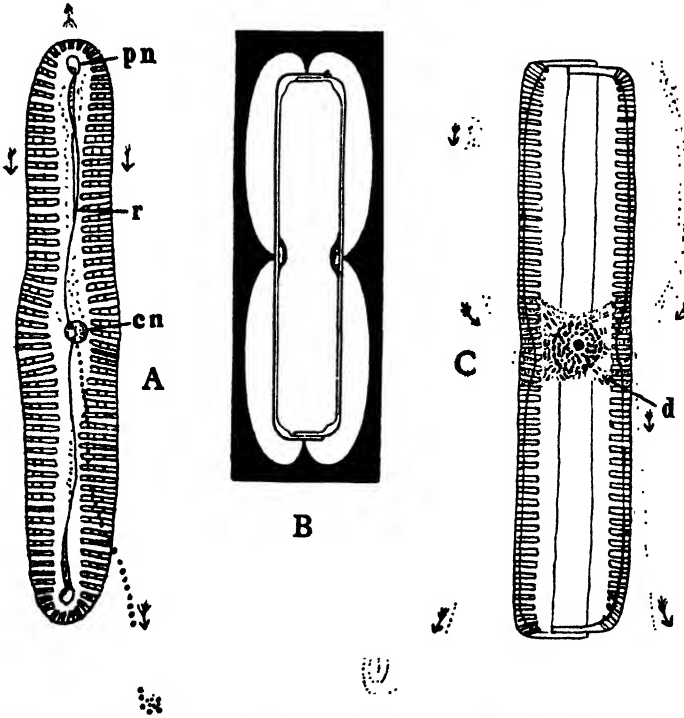

Fig. 197. Movement of *Pinnularia viridis* Kütz. (diagrams after Lauterborn from Oltmanns); A, valve- and C, girdle-views, the dots indicating threads of mucilage with adhering sepia particles, the arrows showing the direction of movement of the latter; B, a frustule in girdle-view placed in sepia. *cn*, central nodules; *d*, rod-shaped bodies near nucleus; *pn*, polar nodules; *r*, raphe.

The existence of these currents has been demonstrated by placing Diatoms in water containing sepia or suspended carmine. In either case, when seen in valve-view (fig. 197 A), the particles are found to glide from the anterior (in the sense of the movement) polar nodule towards the central one, where they exhibit a slight massing, to be subsequently projected backwards and outwards as a fine thread forming an acute angle with the valve and terminating in another accumulation (fig. 197 A). When frustules in motion are observed in girdle-view, they are often seen to be surrounded by a zone of soft mucilage which narrows to a point at the two ends of the individual, as well as at the central nodules (fig. 197 B). The particles of sepia streaming from the anterior pole to the central nodule lie at the periphery of this zone (fig. 197 C), while the backwardly directed thread appears as in the valve-view. This thread is regarded by Müller ((144) (1893, 1894)) as an artefact due to agglutination of the sepia- or carmine-particles by the mucilage, whilst Lauterborn ((114), (115) p. 113) interprets it as a special thread of denser mucilage protruded from the central pores and propelling the individual forwards. The very rapid movements of some Diatoms would, however, necessitate an excretion of mucilage at a rate and in such quantity as seems unbelievable; moreover, such a thread of denser mucilage has not so far been demonstrated by any method of staining. In many small Diatoms the thread-like arrangement of the sepia-particles is by no means always recognisable ((87) p. 134).

According to Müller's view the distribution of the foreign particles is an outcome of the streams in the raphe-system. The massing at the central nodule results from a slowing-down of the plasma-stream at the point where it penetrates into the narrow and wound canals connecting inner and outer fissures (cf. fig. 194 F). At the posterior nodule with its much wider canals there is no such resistance and consequently no accumulation of the foreign particles. Liebisch ((118) p. 52), believing that the internal pectin membrane (cf. p. 565) altogether shuts off the protoplast from the exterior, is of the opinion that the fluid traversing the raphe is water. These water-streams, it is suggested, might arise by slight contractions of the protoplast in the region of the central nodule whereby water would be sucked in through the latter, while a slight undulatory contraction of the protoplast would serve to drive the water through the inner raphe-fissure to the poles. At present, however, no actual facts are available to support these hypotheses, and Cholnoky (27) seems to have given a fairly convincing proof of the fact that the raphe is an actual aperture by demonstrating the escape of cytoplasm from it on treatment of the cells with hypotonic solutions.

In the forms provided with a canal-raphe the phenomena are probably less complex and, where the raphe is continuous, there may be a simple cytoplasmic stream. The function of the apertures or canals leading into this raphe from the interior of the cell is still obscure. The view, put forward especially by Schultze (204) and

Pfitzer ((179) p. 177), that the movement of the cytoplasm in the raphe only admits of creeping along a surface is negatived by the fact that for the performance of movements a substratum is not necessary; moreover, many Naviculoideae exhibit motion when their girdle is in contact with a substratum, in which case any co-operation of the raphe on the valve-faces in a creeping movement is out of the question (cf. also (238)). It seems unnecessary to discuss the older views, attributing the movement to the passage of osmotic currents through the wall (Naegeli, Mereschkowsky) or to the protrusion of flagella or pseudopodia through the raphe (Ehrenberg, Cox, Bütschli).

THE PROTOPLAST

The cytoplasm usually forms a thin lining layer which extends into all the open cavities within the wall and in pennate forms often shows a greater thickness at the poles (fig. 198 D, J). The vacuole is commonly bridged by a conspicuous strand connecting the centre-points of the two valves and occupied by the nucleus (fig. 198 G); in pennate forms this bridge divides the vacuole into two parts (fig. 198 D, F, J). In many Centric Diatoms, however, the nucleus lies in the lining cytoplasm apposed to one of the valves and in such cases the transverse bridge may be lacking and the vacuole traversed by numerous fine cytoplasmic strands (cf. fig. 199 F). Movement of the cytoplasm is conspicuous only in *Rhizosolenia* (38). Korschikoff (110) has demonstrated the presence of contractile vacuoles in the cells of this genus (fig. 199 G, *v*), while Pascher (166) has observed them during division in a species of *Nitzschia*.

A very weak solution of methylene blue will bring out the *nucleus* in the living Diatom, staining it clearly before the rest of the protoplast is coloured. In shape it is rounded or oval or, in pennate forms, commonly reniform (fig. 189 E). The resting nucleus shows minute chromatin granules (fig. 204 K) and contains one or several nucleoli; local denser aggregations of chromatin granules often occur ((23), (50) p. 501). In several genera (perhaps in all?) one or two centrosomes are found in the neighbourhood of the nucleus (cf. p. 611 and fig. 204). In *Surirella* ((115) p. 54) (fig. 189 E, *c*), *Cocconeis placentula* (47) and others (33) the centrosome lies in a hollow to one side of the kidney-shaped nucleus.

The *chromatophores*[1] vary in colour from yellow to olive-green or brown. Forms living in shade (e.g. the numerous mud-inhabiting species) are usually dark-coloured, whilst plankton-diatoms are often more or less lemon-yellow. Freshwater epiphytic forms may, if organic nutriment is available, develop a green colour (35).[2] Fluores-

[1] See (22), (57), (71), (90–92), (115) p. 24, (123), (160), (198).

[2] Stanbury (222 *a*) records chromatic adaptation in *Nitzschia*.

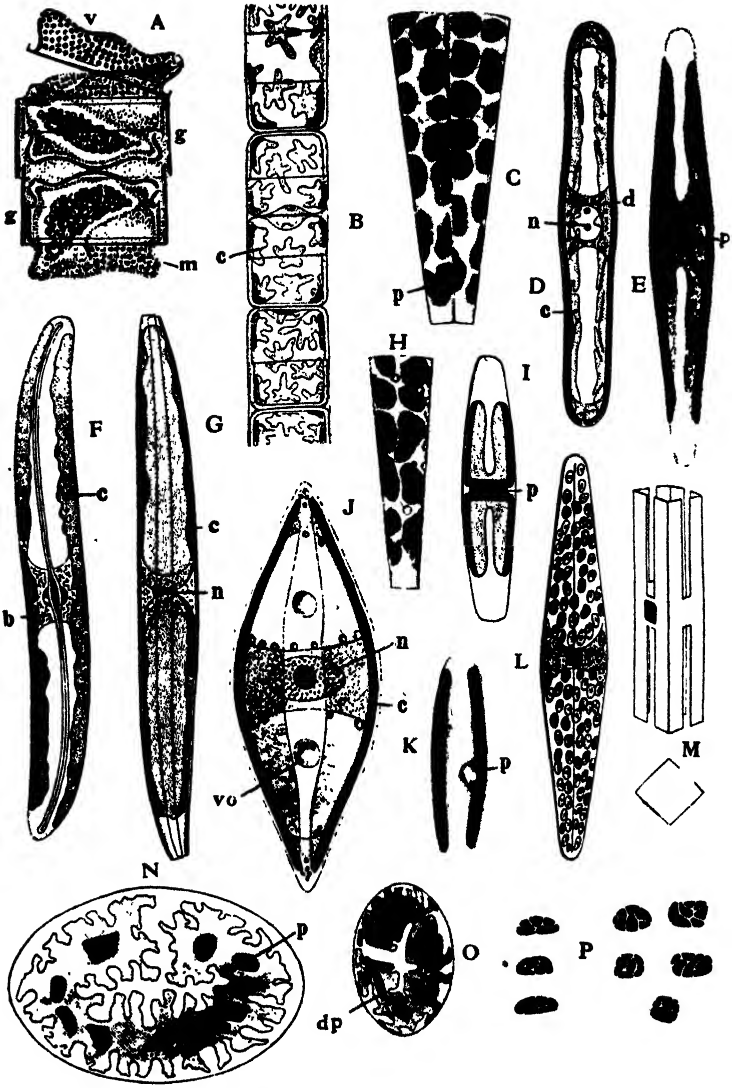

Fig. 198. Chromatophores, etc. of Diatoms. A, *Triceratium antediluvianum* (Ehrenb.) Grun., valves detached showing the pectin-membrane (*m*) with its markings. B, *Melosira arenaria* Moore. C, H, *Meridion circulare* (Grev.) Ag., cells in girdle-view. D, *Pinnularia major* Kütz. E, M, P, *Gomphonema*

cence has been recorded in various diatoms (3, 119). *Melosira Roeseana*, which commonly occurs on rocks subjected to trickling water and favours places with diffuse illumination (237), at times reflects a greenish light (202).

With few exceptions the chromatophores are parietal. The majority of Centrales possess numerous chromatophores, taking the form of minute granules (e.g. *Biddulphia*, fig. 199 F) or, in other cases, of larger, sometimes lobed discs (*Melosira*, fig. 198 B); they are usually apposed to the valves, but lie next to the girdles in the colonial forms. Among Pennales this type is not so frequently encountered, being found most commonly in the Araphideae, i.e. the less specialised forms (*Meridion*, fig. 198 C, H; species of *Fragilaria*; and the marine *Synedras* (60), fig. 207, H, I). In certain species of *Nitzschia* there are numerous band-shaped chromatophores (90–92).

In many of the more advanced Pennate Diatoms we find large plate-like, often extensively lobed chromatophores occupying a large part of the lining cytoplasm and not uncommonly perforated at various points (fig. 198). Where septa occur within the frustules, lobes of the chromatophores usually extend into the chambers produced by them. Among Centric Diatoms this (placochromatic) type is found, for example, in some species of *Chaetoceras* and *Sceletonema*.

The Achnanthaceae have generally a single chromatophore in the shape of a thick plate apposed to the convex valve which bears the pseudoraphe; in *Cocconeis* (fig. 198 N, O) this may be richly lobed. In the Naviculaceae (*Pinnularia*, fig. 198 D; *Navicula*, fig. 198 J; *Pleurosigma*, fig. 198 F, G) there are mostly two large plate-like chromatophores principally apposed to the girdles but extending more or less markedly on to the valve-faces, although leaving the line of the raphe clear; sometimes the two are connected by a median bridge. Some of the smaller species of *Navicula* (fig. 198 K) have a single chromatophore apposed to one of the valves and spreading on to the two girdles (57). *Gomphonema* (fig. 198 E, M) likewise has only a single often deeply incised chromatophore, the median portion of which lies against one of the girdles, while the rest spreads over on to the valve-faces and most of the other girdle. In *Nitzschia* a similar state of affairs often obtains, although the side-pieces of the chromatophore do not

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parvulum (Kütz.) Grun. var. *micropus* (Kütz.) Cl.; E, valve-view; M, diagrams of chromatophore, the lower one a transverse section; P, compound pyrenoids. F, G, *Pleurosigma Spenceri* W. Sm.; F, valve- and G, girdle-views. I, *Cymbella aspera* (Ehrenb.) Cl. J, *Navicula cuspidata* Kütz., valve-view. K, *N. seminulum* Grun., valve-view. L, *Pleurosigma giganteum* Grun., valve-view. N, O, *Cocconeis placentula* Ehrenb. var. *lineata* (Ehrenb.) Cl., valve-views. *b*, median cytoplasmic bridge; *c*, chromatophores; *d*, rod-shaped bodies around nucleus; *dp*, double pyrenoid; *g*, girdle; *n*, nucleus; *p*, pyrenoid; *v*, valve; *vo*, volutin. (A after Liebisch; B, F, G after Karsten; D, I after Heinzerling; J after Lauterborn; the rest after Geitler.)

extend on to the opposite girdle; in some species of this genus, however, the chromatophore is stretched out diagonally from keel to keel. The two chromatophores of *Surirella* (fig. 189 A, *p*, p. 572), apposed to the respective valve-faces, extend as richly lobed structures on to the girdles, whilst lobes also penetrate into the canals connecting with the raphe (fig. 189 D–F, *p*); as in Naviculaceae the two chromatophores are often connected by a transverse bridge (fig. 189 E).

It must be realised, however, that in the larger genera there is often great diversity among the individual species. Thus, in *Pleurosigma* (94) there may be two almost entire plates (fig. 198 F, G), or two or four much-lobed structures or finally (*P. giganteum*, fig. 198 L) numerous small discs. Similar variations are found among the species of *Achnanthes*, *Amphora*, and *Nitzschia*. The movements of the chromatophores of Diatoms in relation to illumination and during division have been studied especially by Senn (216–218).

In a considerable number of cases the chromatophores contain naked spherical or lenticular *pyrenoids* ((199) p. 114) appearing as bright glistening bodies which often project from the internal face as rounded elevations (fig. 198 E, K, *p*). They are not commonly found in Centrales ((66) p. 537) and are variable in their occurrence, even among species of the same genus, in Pennales; thus, they are stated to be lacking in most species of *Navicula*, although present in the closely allied *Pinnularia*, whilst in *Pleurosigma* only some species possess them. In some cases there is a single large pyrenoid, whilst in others there are several (*Pleurosigma*, Nitzschioideae, cf. also fig. 198 N).

Mereschkowsky (126) records pyrenoids which had partially or entirely separated from the chromatophores, appearing as free colourless bodies on their inner surface; according to Geitler (46), however, this observation is due to confusion with oil-drops. *Gomphonema parvulum* var. *micropus* possesses a compound pyrenoid ((57) p. 49) consisting of a number of irregular polyhedral pieces (fig. 198 P), while double pyrenoids are known in *Cocconeis* (fig. 198 O, *dp*).

The marine members of the Tabellariaceae possess very characteristic stellate chromatophores with central pyrenoids (94). In *Grammatophora marina* (fig. 199 B) there are only one or two, whilst in *Rhabdonema arcuatum* (fig. 199 A) they are numerous. In the latter, moreover, the pyrenoid is not homogeneous, as in *Grammatophora*, but consists of as many fragments as there are segments to the stellate chromatophore, one pyrenoid being located at the inner end of each ray. The same is the case in *Striatella* (133, 198) (fig. 199 C), where the two chromatophores appear as half-stars, axially placed on either side of the nucleus (*n*). Such cases are possibly better interpreted as star-shaped aggregates of band-shaped chromatophores, with pyrenoids at their inner ends.

Surveying the chromatophores of Diatoms as a whole, it can hardly be doubted that the single large plate represents the primitive type which has gradually become lobed and divided up to form the numerous chromatophores present in many genera. The peculiar

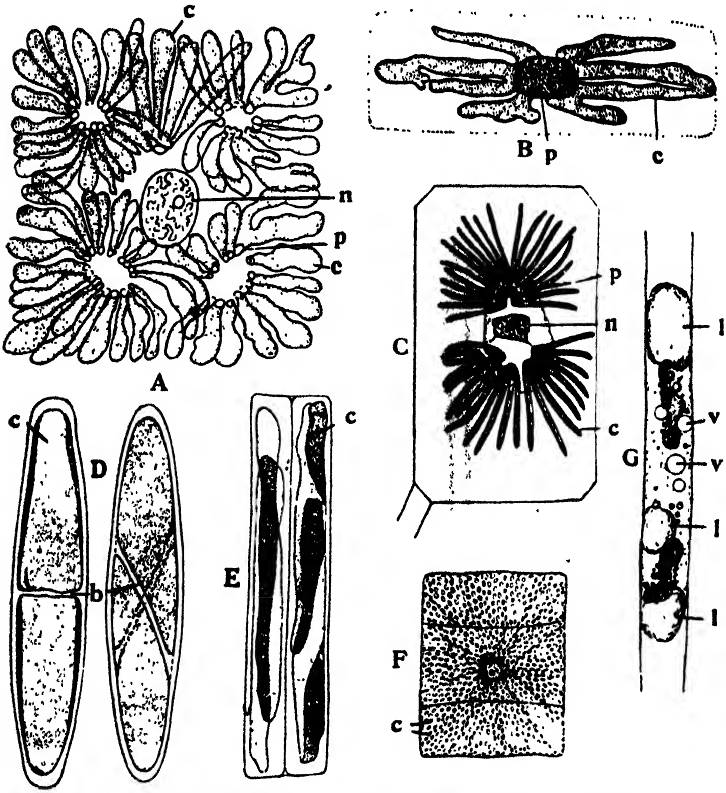

Fig. 199. Chromatophores, etc. A, *Rhabdonema arcuatum* (Lyngb.) Kütz., stellate arrangement of chromatophores. B, *Grammatophora marina* (Lyngb.) Kütz., single chromatophore. C, *Striatella unipunctata* (Lyngb.) Ag. D, E, *Navicula oblonga* Kütz., fission and displacement of chromatophores during division, D valve- and E girdle-views; D, on the left transverse division of chromatophore which has shifted to the valve-face, on the right the half-chromatophores growing past one another (dotted lines those belonging to the other valve); E, the new chromatophores already occupying the greater part of the girdle-surface. F, *Biddulphia pellucida* Castrac., granular chromatophores. G, *Rhizosolenia longiseta* Zach., central part of cell. *b*, line of fission of chromatophore; *c*, chromatophore; *l*, leucosin; *n*, nucleus; *p*, pyrenoid; *v*, vacuole. (A, B after Karsten; C after Schmitz; D, E after Ott; F after Senn; G after Korschikoff.)

minute granular chromatophores met with in many Centrales (fig 199 F) and also found in some pennate forms are without parallel in other classes of the Algae. The most highly evolved type thus occurs in the Centrales, and this is in agreement with the marked structural complexity shown by their cell-membranes.

The nature of the pigments contained in the chromatophores of Diatoms is yet scarcely settled. Apart from Kohl (106), who maintained that the pigments were the same as in higher plants, though occurring in different proportions, the older investigators believed that the usual pigments were masked by the presence of an accessory brown one, *diatomin*, soluble in water after the death of the cell and very similar to, or perhaps identical with, the fucoxanthin of Phaeophyceae. This view finds support in Kylin's conclusions (113), who believes to have established spectroscopically the presence of the same carotinoid pigments as in Phaeophyceae, viz. carotin, two modifications of xanthophyll, and fucoxanthin α and β. Molisch ((136), (137) p. 257), however, is of the opinion that Diatoms contain a brown modification of chlorophyll (*phaeophyll*), similar to that which he assumes to be present in Phaeophyceae, accompanied by carotin and xanthophyll, as well as fucoxanthin (Molisch's leucocyanin). His phaeophyll is stated to change readily into chlorophyll after death.

A considerable number of Diatoms are known to favour waters with some organic content and some (e.g. *Pleurosigma*) are found abundantly where extensive decay is taking place. In artificial cultures too provision of organic nitrogen (especially as asparagin and leucin) has proved beneficial (185, 186). Some Diatoms, however, thrive in inorganic culture media (173), although Allen (1) found that *Thalassiosira gravida* only prospered in artificial sea-water if a small amount of natural sea-water was added (cf. also (68 *a*)). He concluded that this was due to the presence in the sea-water of minute quantities of some specific substance essential for growth. According to Richter ((186) p. 94) *Nitzschia palea*, *inter alia*, does not multiply in pure cultures in the dark, no matter what organic material is provided.

Karsten (96) established that certain forms (*Nitzschia palea*, *Hantzschia amphioxys*), when grown in organic solutions, showed a progressive decrease in the size of the chromatophores combined with a decrease in the intensity of their pigmentation; the reduction took place more rapidly in cultures exposed to light than in those kept in darkness, which Karsten ascribed to the more rapid multiplication of individuals in the former case and failure of the chromatophores to grow after division. At the time of Karsten's investigations pure cultures of Diatoms were not yet feasible, and his results may be due to pathological causes resulting from the presence of Bacteria. Reduction of chromatophores in species of *Nitzschia* has been observed also by Cholnoky (22) and others. A number of species of this genus normally occur as colourless forms in nature (*N. putrida*, *N. leucosigma*), chromatophores being completely absent (cf. (10));[1] attempts to induce their development by appropriate conditions of culture have not been successful.

A peculiar blue-coloured *Navicula* (*N. ostrearia*), commonly found in oyster-beds and in tanks in which oysters are cultivated, has been investigated by Sauvageau and others (45, 135, 184, 189). The pigment, which is water-soluble, is found in the cytoplasm and the vacuole, but not in the chromatophore; it has nothing in common with the pigment of the Blue-Green Algae (17). The oysters that feed on this Diatom assume the blue colour.

The products of photosynthesis would appear in the main to occur as drops of fatty oil which are usually conspicuous in the cells when plenty of nutritive material is available and often accumulate in large quantities when growth and multiplication are arrested (9). Side by side with them other globules (Bütschli's globules (115) p. 30) occur which have been identified as ***volutin*** by A. Meyer ((71) p. 18, (127) p. 139). They are faintly bluish with a dull lustre, do not stain with osmic acid, and are insoluble in alcohol and ether; in living cells treated with methylene blue they take on a deep reddish violet tint. In many cases the volutin-globules are distributed over the whole cell, but in others they occupy a definite position which is characteristic for the species. Thus, in *Navicula cuspidata* (fig. 198 J) and often also in *Amphora ovalis*, a large volutin-globule (*vo*) is found on either side of the central protoplasmic bridge, beneath the raphe, whilst in *Nitzschia sigmoidea* the globules occur at the ends of the chromatophores.

Heinzerling ((71) p. 19) showed that in some cases the contents of the globules are viscous and fluid, but that in others they are crystalline and doubly refractive. Kolbe ((108) p. 71) describes those of *Navicula oblonga* as consisting of a fat-globule enveloped by a thick layer of volutin. During nuclear division the globules usually disappear, but reappear after division is completed. According to Korschikoff (110) leucosin (p. 508) is also present in Diatoms (fig. 199 G, *l*). The nucleus is commonly surrounded by small rods or plates ((71) p. 16, (115)) grouped in pairs (fig. 197 C, 198 D, *d*), the nature and function of which are unknown; they are well seen in some of the larger *Pinnularias*. According to Lauterborn they occur most abundantly during cell-division.

COLONIAL AND EPIPHYTIC DIATOMS

A large number of Diatoms have adopted a colonial or epiphytic habit, the junction of the individual frustules or attachment to a substratum being effected with the help of mucilage, often secreted

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[1] Prowazek's (183) *Synedra hyalina* is probably a species of *Nitzschia*.

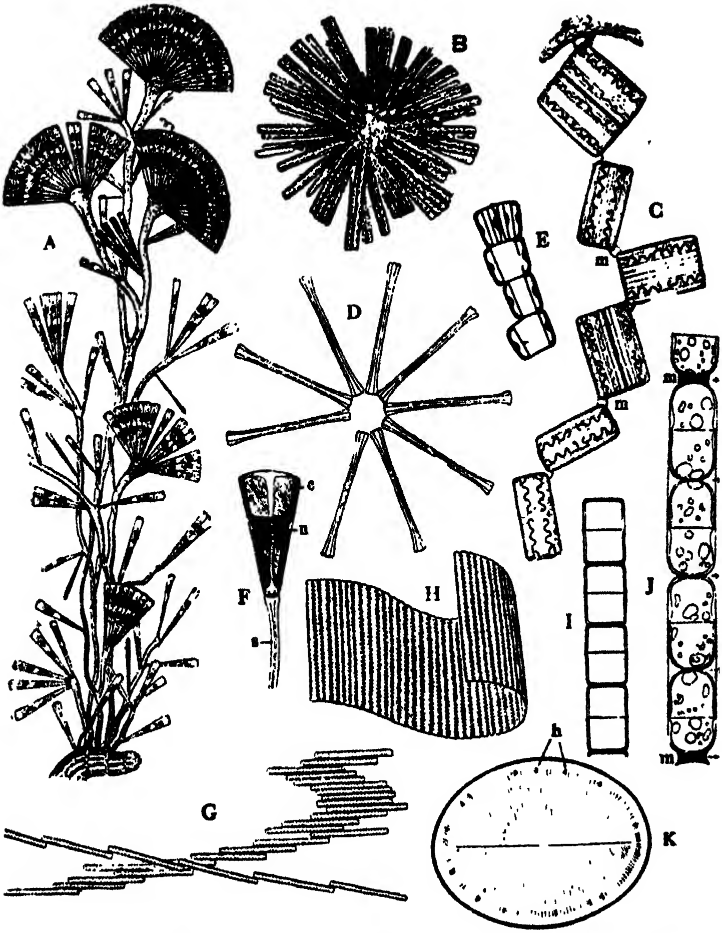

Fig. 200. Colonial and epiphytic Diatoms. A, *Licmophora flabellata* (Carm.) Ag. B, *Synedra ulna* (Nitzsch) Ehrenb. C, *Grammatophora serpentina* Ralfs. D, *Asterionella gracillima* Heib. E, *Pinnularia socialis* Palmer, polar view of a dividing colony, in the two middle cells division only beginning. F, *Gomphonema constrictum* Ehrenb., girdle-view. G, H, *Bacillaria paradoxa* Gmel.; G, drawn out; H, contracted. I, *Melosira varians* Ag. J, *M. Jürgensii* Ag. K, *Cocconeis placentula* Ehrenb., lower valve. *c*, chromatophore; *h*, process; *m*, mucilage; *n*, nucleus; *s*, mucilage-stalk. (D, I after West; E, J, K after Hustedt; F after Pfitzer; the rest after W. Smith.)

through relatively large, readily recognisable pores (fig. 202 C, D, G, H, *p*). The modes of colony-formation are especially diverse in Centrales.

Some of the commonest epiphytes occur attached along their whole surface, in *Cocconeis* (fig. 187 G, H) by means of the raphe-bearing valve, in *Epithemia* (fig. 191 A) and *Amphora* by means of the ventral girdles; in these cases the cementing material is difficult to demonstrate. In *Cocconeis placentula*, however, the lower valve bears minute processes (fig. 200 K, *h*) which are stated to serve for attachment ((233) pp. 46, 50). The connecting mucilage is likewise difficult to recognise in the filamentous colonies formed by many Diatoms (e.g. *Melosira*, *Fragilaria*, *Eunotia* (*Himantidium*), etc., fig. 200 I), where the frustules are joined by a larger or smaller area of their valve-faces, although in many of the *Melosiras* with convex valves the intervening pads of mucilage are plainly visible after staining (fig. 200 J, *m*). In a number of the marine pelagic *Nitzschias* only the apices of the frustules are joined together ((67) p. 129), while in the unique *Bacillaria paradoxa* (fig. 200 G, H) the surface of contact varies as the frustules glide over one another (cf. p. 590).

Pinnularia socialis (79, 162) forms four- or eight-celled colonies in which, however, the individuals are united by their girdles and not by their valve-faces (fig. 200 E). Division of individuals takes place as usual along the valvar plane, not necessarily at the same time in all the cells of a colony (fig. 200 E), but when all have divided the colony simply splits into two comprising the same number of individuals as the parent. As Hustedt points out, it is difficult to conceive how this peculiar type of colony originated in the first place.

In many Diatoms the secretion of connecting mucilage is more localised. Familiar examples are the zigzag colonies of *Grammatophora* (fig. 200 C), *Diatoma*, and *Tabellaria* (fig. 190 H), where the frustules are joined by mucilage-cushions (*m*) at the corners, the basal one being fastened in the same manner to a substratum (fig. 200 C). In some *Melosiras* with marked mucilage-pads between the successive individuals the basal frustule may be fixed in the same way to a foreign object. In other cases (*Asterionella*, fig. 200 D; *Tabellaria*) the individuals are united by basal mucilage-cushions to form characteristic stellate free-floating groups. Wesenburg-Lund (230) has shown that the colonies of *Tabellaria* and *Diatoma* are at first found attached as zigzag chains, but later in the season appear in the plankton largely as stellate aggregates, so that the two types of colonies are evidently related. In *Gomphonema* and some species of *Cymbella* the individuals are borne singly fixed by their narrower ends (fig. 200 F) on a system of branched hyaline mucilage-stalks, attached to various substrata, whilst in the similar colonies of *Licmophora*

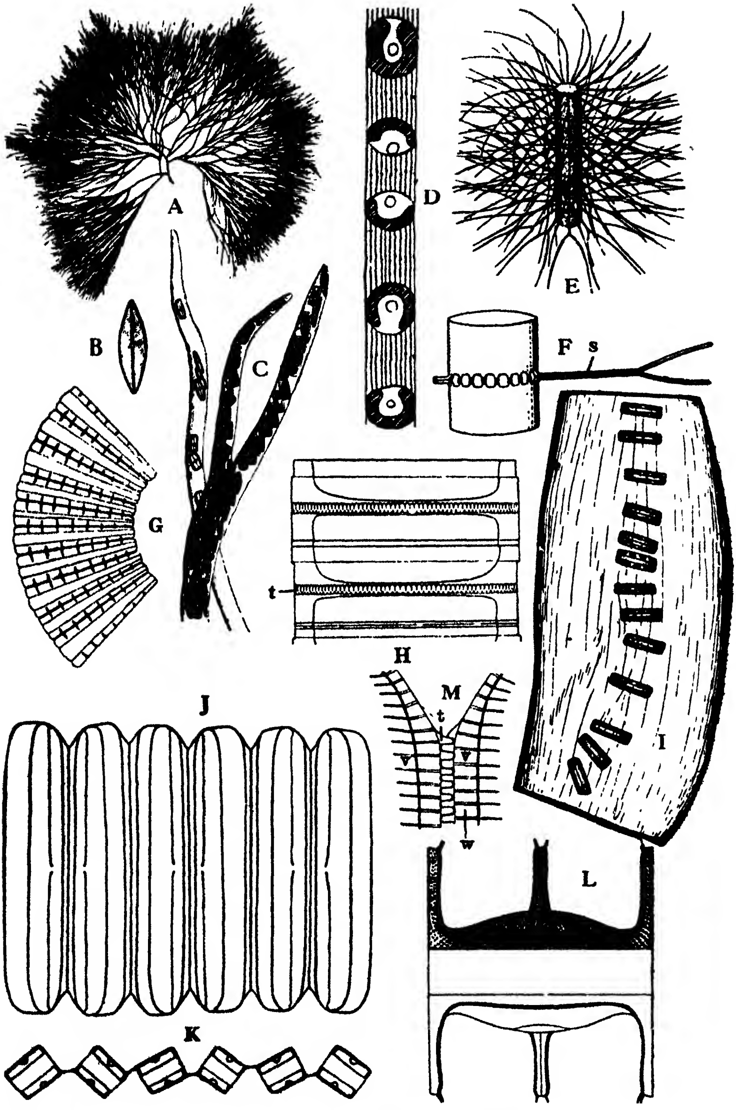

Fig. 201. Colonial Diatoms. A–C, *Navicula* (*Schizonema*) *Grevillei* Ag.; A, habit; B, single individual, valve-view; C, small part of colony enlarged. D, *Sceletonema costatum* (Grev.) Cl. E, F, *Bacteriastrum varians* Lauder; E, habit; F, part of two frustules in girdle-view. G, *Meridion circulare* (Grev.)

(fig. 200 A) the branches bear fan-shaped groups of frustules. According to Cholnoky(25) the stalks consist of an outer envelope which surrounds a mass of mucilage in *Cymbella*, while in *Gomphonema* there is an inner lamella which broadens out beneath each individual. In some *Gomphonemas*, as well as in *Rhoicosphenia*, each individual occupies the end of an unbranched stalk or mucilage-cushion and the same habit is seen in the bent frustules of *Achnanthes*, which are often joined to form ribbons, and in many species of *Cymbella*. A number of *Synedras* occur attached in tufts by means of mucilage-cushions (fig. 200 B).

Colonies of a different nature are seen in some species of *Navicula* (sections *Frustulia*, *Schizonema*, fig. 201 A–C), *Cymbella* (*Encyonema*), and *Nitzschia* (*Homoeocladia*(44, 45)). Here large numbers of individuals occur enclosed in a common tubular mucilage-envelope which is sometimes richly branched; this condition is particularly frequent in marine forms. Within the envelopes the individuals are freely motile, but they can also occur as solitary cells. According to Karsten ((94), cf. also (234)) the first individual of such a colony secretes a wide tube of enveloping mucilage within which multiplication takes place, the daughter-individuals producing more and more mucilage. Moebius(134) and Cholnoky(30) record cases in which two distinct species occur within such colonies, while Germain(61) describes the presence of *Nitzschias* within the mucilage-tubes of Naviculaceae. In *Cyclotella planctonica* (fig. 201 I) the individuals are often found at more or less regular intervals in a wide cylindrical mucilage-envelope, while in species of *Thalassiosira* and *Navicula* (*Dickieia*) large numbers of frustules may lie embedded in foliaceous mucilage-expanses.

In other Diatoms the individuals of the colonies are united by special outgrowths of the cells, although there is no doubt also some connecting mucilage.

In *Pinnularia Debesii*(79) the individuals are joined by interlocking teeth (*t*) developed along the winged edges of the valves (fig. 201 M), the individuals presenting either their girdles or their valves or the edges of the latter to the observer (fig. 201 J, K). As a general rule successive pairs of individuals are joined by alternate valve-edges (fig. 201 K), and it is only on these edges that the connecting mechanism is developed. A similar mode of union is found in *Melosira arenaria* (fig. 201 H) and

Ag. H, *Melosira arenaria* Moore. I, *Cyclotella planctonica* Brunnth. J, K, M, *Pinnularia Debesii* Hust.; J, surface-view, frustules seen from edge; K, diagrammatic transapical section of same; M, connection between two valves. L, *Hemiaulus regina* Heib., girdle-view. *s*, seta; *t*, tooth; *v*, valve; *w*, wing of same. (A–C after W. Smith; D after Karsten; E, F after Schütt; G after West; L after Heiberg; the rest after Hustedt.)

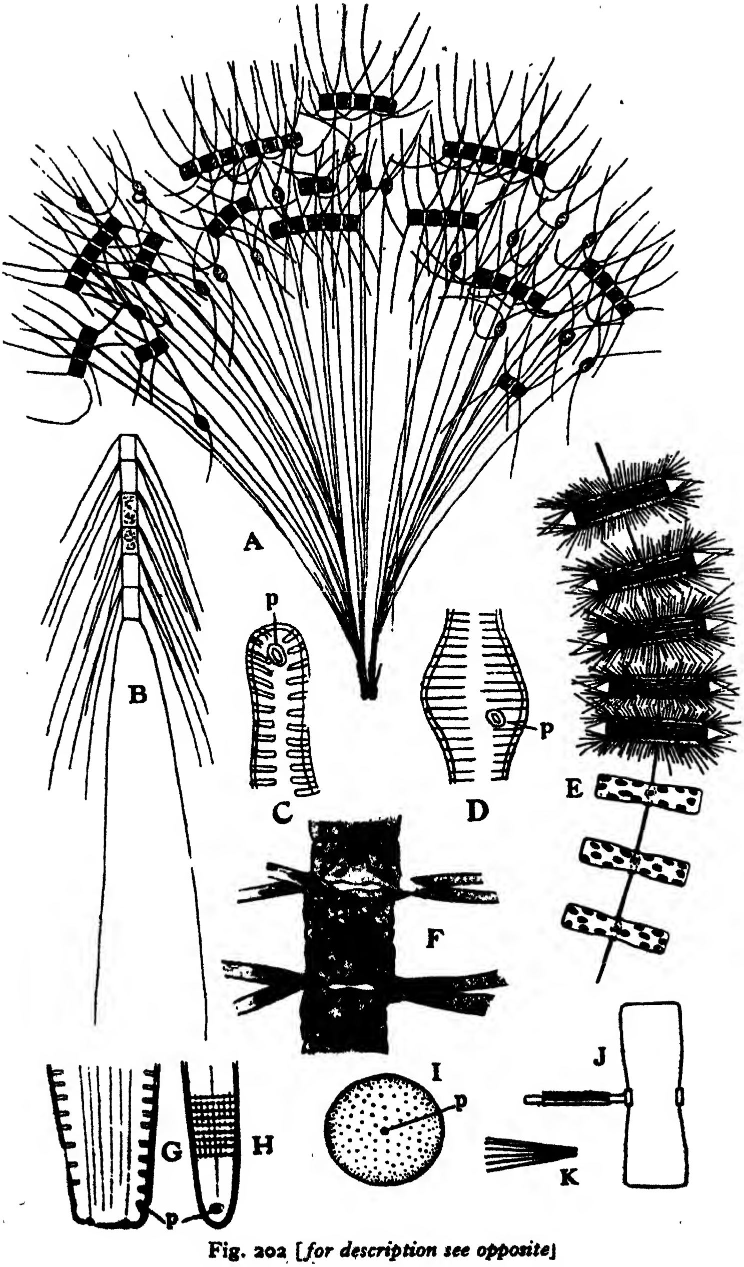

Fig. 202 [*for description see opposite*]

other species of the genus where the teeth are, however, developed all round the edges of the circular valves. In *Hemiaulus* the corners of the valves are produced into processes running parallel with the long axis of the individual, and at the tip of each process are claw-like spines by means of which adjacent frustules interlock (fig. 201 L).

The marine genera *Stephanopyxis* and *Sceletonema* (fig. 201 D)(16) have the individuals joined by a number of silicified processes, very delicate in the latter, arising near the edge of the valve-face, each process being traversed by a fine canal through which no doubt the cementing material that joins their tips is secreted. In the case of *Sceletonema costatum* Karsten(93) showed that the connecting processes develop to their full length only in moving water. A somewhat similar method of colony-formation obtains in *Cyclotella socialis*(211), where, however, only loose and irregular aggregates are formed and the processes are not silicified.

A different method of junction by means of outgrowths on the valves is seen in the widely distributed marine plankton-genus *Bacteriastrum*(171) (fig. 201 E). Here the setae which arise in a ring from the edges of the valves, at first run parallel to the long axis of the cell, but almost immediately bend out at a right angle. The frustules are united to form threads by the joining together of the proximal portions of the setae on adjacent valves for a considerable distance (fig. 201 F). The individuals of *Chaetoceras* (fig. 202 B) are joined in much the same way with the help of the basal portions of the pairs of long horns that arise from the poles of the elliptical valves(207) and which are so disposed that those of adjacent frustules cross one another (fig. 202 F). A very remarkable case is afforded by *C. socialis* (fig. 202 A) in which one horn of each individual is of enormous length, all the elongate processes arising from a group of few-celled colonies converging to a point where they are united, the whole aggregate being embedded in a common mass of mucilage(122).

In many Pennate Diatoms the mucilage responsible for attachment to a substratum or for joining one individual of a colony to another is secreted through large obvious pores, usually placed singly near one or both poles of the valves and generally occupying thickenings of the wall which project markedly (cf. fig. 202 G) on the inner

Fig. 202. Colonial Diatoms. A, *Chaetoceras socialis* Laud. B, *C subtilis* Cl. C, *Synedra splendens* Kütz. (*ulna*?), apex of valve with mucilage-pore (*p*). D, *Tabellaria fenestrata* (Lyngb.) Kütz., central part of valve with mucilage-pore (*p*). E, I–K, *Thalassiosira gravida* Cl.; E, habit; I, valve-view showing pores; J, girdle-view with mucilage-strand; K, the separate threads composing the latter. F, *Chaetoceras Castracanei* Karst., showing crossing of horns. G, H, *Licmophora*, mucilage-pores; G, girdle- and H, valve-views. *p*, mucilage-pore. (A, E, I–K after Mangin; B after Meunier; F after Karsten; the rest after O. Müller.)

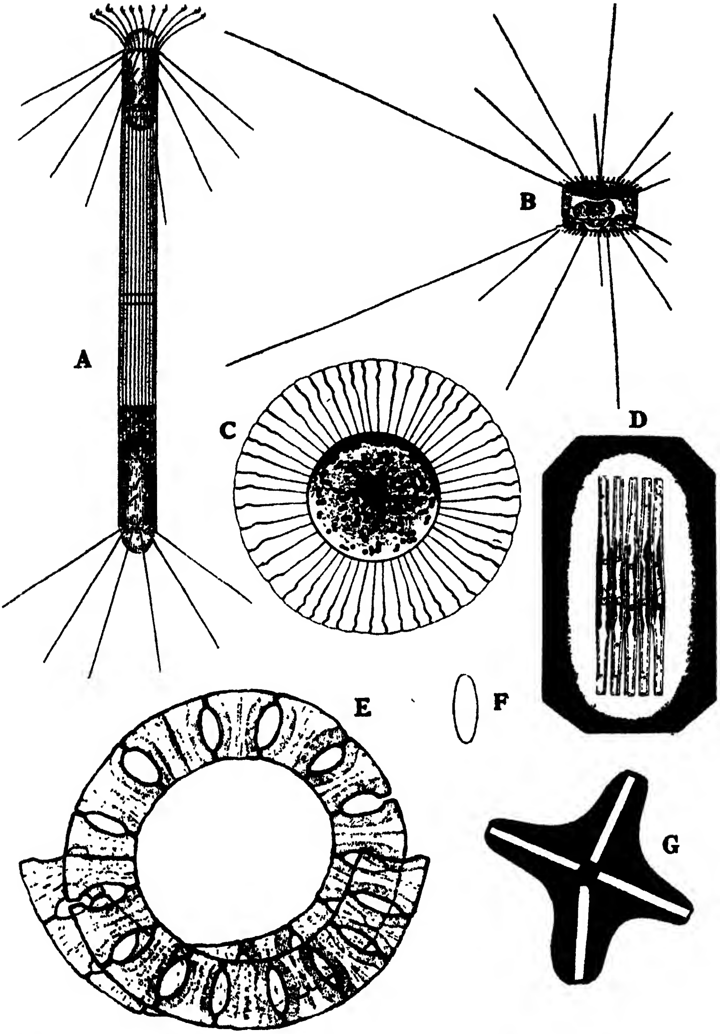

Fig. 203. Plankton Diatoms. A, *Corethron Valdiviae* (Schimp.) Karst., complete cell. B, *Stephanodiscus Hantzschii* Grun. C, *Planktoniella Sol* (Wall.) Schütt, valve-view. D, *Fragilaria crotonensis* (A. M. Edw.) Kitton, small colony in sepia showing mucilage-envelope. E, F, *Eucampia zodiacus* Ehrenb.; E, colony; F, individual in valve-view. G, *Tabellaria* sp., mucilage-envelope (black). (A after Karsten; B, D after Schröder; C after Schütt; E, F after W. Smith; G after Naumann.)

surface (62, 78, 86, 150). Thus, in *Synedra* (fig. 202 C) such a pore is found at either pole, while in *Licmophora* (fig. 202 G, H) there is often only a single one at the narrow end of the valve. Among Centric Diatoms obvious mucilage-pores are not always recognisable, but it can hardly be doubted that the fine pores which have been demonstrated in the membrane of several forms are the apertures through which secretion of mucilage occurs. In *Thalassiosira*, where the successive flat circular frustules are joined by a more or less delicate thread of mucilage arising from the centre of the valve-face (fig. 202 E), a large obvious mucilage-pore is detectable in this position in some cases (fig. 202 I, *p*); in others there are groups of small pores in the centre of the valve, and in this connection it may be noted that in *T. gravida* the connecting strand has been shown to consist of a bundle of threads (fig. 202 J, K) held together by a sheath of cellulose (122). A freshwater species of this genus gives rise to occasional water-flowers (77, 109) due to the entanglement of oxygen-bubbles between the mucilage-threads.

PLANKTON DIATOMS

Many Diatoms lead a pelagic existence, and in the sea they are probably more abundant than any other pelagic plants (208). The diverse shapes encountered among pelagic Diatoms clearly adapt them well to a free-floating existence; such are: the flat discoid form of many Centric Diatoms (fig. 186 F, G); the needle-shape of others (*Rhizosolenia*, fig. 191 H; *Synedra*, fig. 187 N) which reaches its extreme in such a form as *Synedra thalassothrix* (208);[1] and the long filaments, which are sometimes spirally coiled, as in *Eucampia* (fig. 203 E) and some of the freshwater *Melosiras* (159). In many species, moreover, the surface is increased by more or less elongate silicified bristles arising usually from the valve-edge (*Stephanodiscus*, fig. 203 B; *Cyclotella*; *Corethron*, fig. 203 A), while the long horns of the species of *Bacteriastrum* (fig. 201 E) and *Chaetoceras* (fig. 202 A, B) operate in the same way. The stellate colonies of *Asterionella* (fig. 200 D) and *Tabellaria* are a typical feature of the freshwater plankton in many pieces of water.

In *Planktoniella Sol* (fig. 203 C), widely distributed in the oceanic plankton of warmer seas, the epitheca is provided with a broad, hollow, slightly silicified wing divided by septa into a series of chambers. The frequent presence of mucilage-envelopes in plankton-diatoms (figs. 201 I, 203 D) no doubt also aids in flotation, and in some of the species of *Tabellaria* the individuals of the star-shaped

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[1] A peculiar organism of this type is constituted by the triradiate *Centronella* (112, 228) which Bohlin (19) identifies with his *Phaeodactylon* (18). Whether this is really a diatom remains doubtful.

colonies have spread out between them a delicate layer of mucilage (fig. 203 G) so that the whole has the character of a parachute (156, 227). A somewhat similar device has been described for *Chaetoceras decipiens* (7) where a zone of mucilage extends around each individual in the valvar plane. The abundant fat often present in the cells of Diatoms must decrease their specific gravity. Plankton-diatoms often have more delicate valves than the bottom-living forms.

The Pennales are represented in about equal numbers in marine and freshwater plankton, and it is the great preponderance of Centrales in the sea that gives the plankton not only its special stamp, but is also in the main responsible for its extensive development. The colder seas are richer in pelagic Diatoms than the warmer ones. In the oceans a marked horizontal stratification of the diatom-plankton is often recognisable which is in part probably related to the diverse capacity for flotation, but in part also to an attunement to different light-intensities. Thus the Discoideae (p. 640) are usually found in deeper water than the Solenoideae with their better equipment for floating. In the Indian Ocean, where temperature-effects scarcely come into play, the surface-plankton consists of *Chaetoceras*, *Rhizosolenia*, etc., while in the deeper water one finds shade-forms like *Planktoniella* and other Discoideae (98, 101). In northern waters plankton-diatoms are not found in any quantity below about 90 metres, although in tropical seas they may be found at a depth of from 200 to 400 metres.

There is a marked difference between the oceanic plankton, small in amount but with numerous species, and the neritic plankton near the coasts where the larger supply of nutritive salts admits of a more copious development and certain Diatoms characteristic of the littoral region and washed in from the adjacent land are to be encountered. In some regions (e.g. the west coast of Africa), however, ocean currents are responsible for bringing abundant nutriment to the surface, and this is accompanied by the development of a rich diatom-plankton. Pearsall (174) has shown that in the case of freshwater plankton also the maxima of Diatoms are evidently related to the influx of abundant nutritive material into the water. In northern seas there is usually a marked maximum with many different genera (*Thalassiosira*, *Coscinodiscus*, *Chaetoceras*, *Sceletonema*) in the late winter or early spring, and there is often a second maximum in late summer or autumn. *Rhizosolenia* and *Chaetoceras* are the most important forms, of which the latter precedes the former which is found into the summer. *Biddulphia* occurs especially in the autumn (72 a, 116).

CELL-DIVISION

The usual method of multiplication of Diatoms is by means of successive division ((115) p. 58) which takes place generally at night and always transverse to the longitudinal axis of the individual (i.e. in the valvar plane). An increase in the volume of the frustule, conditioning a slight separation of the two thecae, is followed by mitotic division of the nucleus (fig. 204 B, C) and a gradual fission of the protoplast from without inwards in a plane parallel to the valve-faces (fig. 204 C, D). Thereupon new siliceous valves, at first very delicate, are formed over the fresh protoplasmic surfaces (fig. 204 E). The new valves (*v*) are situated within the girdle of the parent-frustule, but as the new connecting-bands develop, those of the parent separate. Thus each daughter-individual consists of a new and an old half, the connecting-band of the old valve overlapping that of the new. Moreover, the hypotheca of the parent becomes the epitheca of one of the daughter-individuals. Since the valves when once mature are incapable of growth, one individual of each successive generation will tend to become reduced in size by the double thickness of a connecting-band. This statement is not strictly true, however, for all forms (cf. p. 616).

The process of nuclear division has been mainly investigated in Pennales and was first fully studied in *Surirella Capronii*[1] by Lauterborn (115). Later work has not supported all his conclusions. According to his account the commencement of nuclear division in *Surirella* is marked by the separation of the centrosome (p. 593) from the nucleus which gradually assumes a rounded form and, together with the centrosome, slowly passes to the broader end of the frustule (fig. 204 B). The centrosome becomes surrounded by marked cytoplasmic radiations (fig. 204 B, *c*) and soon a second small body is recognisable in its neighbourhood which Lauterborn believed to originate from the centrosome by division. This second body undergoes appreciable enlargement and, as it approaches the nucleus, gradually assumes the form of a narrow cylinder (fig. 204 L, *s*).

The chromatin granules in the nucleus become arranged in moniliform threads (fig. 204 B, L) which later form a smooth, much coiled spireme, while the several nucleoli disappear. As the spireme segments into the numerous chromosomes, the cylindrical group of fibres which has originated from the above-mentioned second body penetrates the nuclear cavity and forms the spindle (fig. 204 C, M, *s*) which, as seen in girdle-view, has somewhat of the shape of an hourglass with a circular cross-section. The spindle is therefore extra-

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[1] This species was described by Lauterborn as *Surirella calcarata*, but according to Hustedt ((87) p. 79) it is *S. Capronii*.

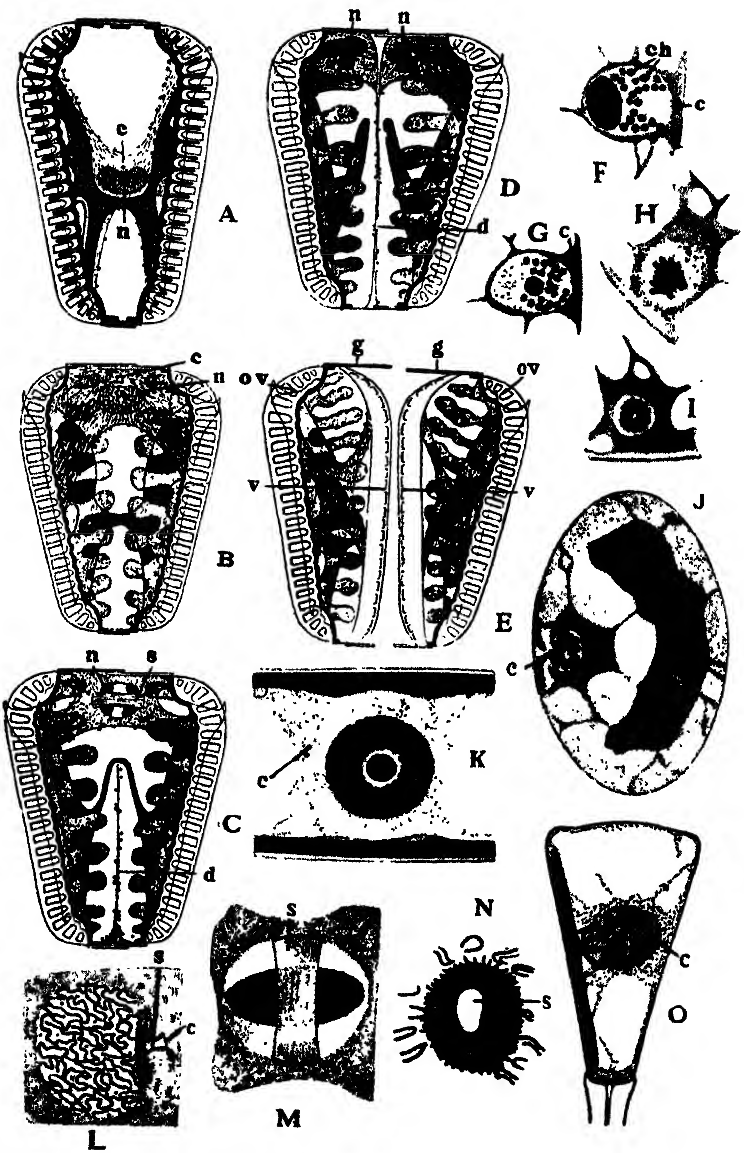

Fig. 204 [*for description see opposite*]

nuclear in origin. Simultaneously the centrosome itself disappears, two new centrosomes being gradually constituted at the broad poles of the spindle. The loop-like chromosomes which are now longitudinally split, become grouped in a hollow ring at the equator and their halves diverge in this form (fig. 204 N), the aperture of the ring gradually narrowing as the poles are approached. Within the daughter-nuclei the chromosomes slowly become resolved into the numerous chromatin granules that are characteristic of the resting nucleus. In many of the Diatoms that have been investigated the chromosomes are short rod-like structures (cf. fig. 204 H).

The peculiar features of the preceding account of nuclear division in *Surirella* are that the spindle is extranuclear in origin and that it is supposed to wander into the nucleus prior to the separation of the chromosomes. Karsten (95) was unable to recognise a centrosome at times other than those of division and he came to the conclusion that the spindle is formed from the centrosome itself (cf. also (9*a*) p. 50). Geitler's description of somatic nuclear division in *Cocconeis placentula* ((47) p. 520) is in essential agreement with this (fig. 204 F–J) and he found some support for the view that the centrosome penetrates into the nucleus in the early stages of mitosis (fig. 204 J). In most other Pennate Diatoms investigated, both by Lauterborn, Karsten (90–92), and more recent workers (23, 54, 58, 60, 124, 235), a definite centrosome has been unrecognisable even during division, although the usual occurrence of cytoplasmic radiations about a definite point near the nucleus has been taken as evidence of its presence ((103) p. 5). The same is true of Ikari's account (89) of nuclear division in *Coscinodiscus* (cf. also (74), (195)). Recently, however, Cholnoky (33) has recorded the occurrence of centrosomes in diverse Pennales (cf. fig. 204 K, O, *c*) and it seems probable that these structures may be universally present in this order, although owing to their small size they are only to be found after very careful fixation.

Cholnoky ((26), (32) p. 101, (33), (33*b*) p. 704) is probably right in

Fig. 204. Cell-division. A–E, L–N, *Surirella Capronii* Bréb. (after Lauterborn); A, non-dividing individual; B, preparation for division; C, nuclear division, protoplast dividing from below upwards; D, nuclear division complete, fission of protoplast complete; E, formation of new valves (*v*), girdle-bands (*g*) separating; L, nucleus in prophase, extranuclear spindle (*s*) developing; M, metaphase, spindle has penetrated nucleus; N, anaphase viewed from one pole. F–I, *Cocconeis placentula* Ehrenb. var. *lineata* Cl. (after Geitler), mitosis; F, G, prophase; H, metaphase; I, equatorial plate viewed from pole. J, *C. placentula* var. *klinographis* Geitl., centrosome (*c*) lengthening into nuclear cavity. K, *Gyrosigma acuminatum* Rabenh. (after Cholnoky), middle of cell with resting nucleus. O, *Gomphonema capitatum* Ehrenb. (after Cholnoky), prophase. *c*, centrosome; *ch*, chromosomes; *d*, line of fission of protoplast; *g*, girdle; *n*, nucleus; *ov*, old valve; *s*, spindle; *v*, new valve.

denying the extranuclear origin of the spindle in Diatoms, and for diverse forms it seems clear that the spindle is formed in a way not differing materially from that of other Algae, except perhaps for the usual presence of centrosomes (cf. also (9 a) p. 51). These, when present, appear to divide and to take up the usual position at the poles of the spindle (fig. 204 O). A reinvestigation of *Surirella* would probably, with the better methods now available, afford results in line with this conclusion. The peculiar mode of spindle-formation in Diatoms would scarcely have been so long accepted had the work on *Surirella* not been undertaken by so excellent an investigator as Lauterborn.

In *Biddulphia sinensis* (193) and diverse other Centrales (195) Schmidt records an intranuclear spindle whose beginnings have not been traced. In his earlier papers he describes a very special type of spindle and other peculiar features in these forms, but in a recent contribution (196 a) many of the earlier statements are withdrawn. Although the spindle is not specifically dealt with, one may doubt the accuracy of the earlier description, the more as Cholnoky's recent study (33 b) of nuclear division in *Melosira arenaria* (fig. 205 F–I) displays a perfectly normal spindle. Centrosomes were not recognised here. The spindle in many Centrales appears to lengthen progressively during mitosis.

Richly lobed chromatophores usually become somewhat simplified prior to division by the drawing in of many of the lobes (36, 160). The two large chromatophores found in many Naviculaceae undergo transverse division and shift to the valve-faces either before (fig. 199 D) or after division. When the new valves have been formed the half chromatophores grow obliquely 'past' one another and then gradually assume their normal position on the girdles. In *Synedra ulna*, according to Senn (217), after transverse division of the chromatophores which are here apposed to the valves, one half remains *in situ*, whilst the other gradually shifts over the girdle on to the new valve-face, in the meanwhile growing to its mature size. Single chromatophores usually undergo longitudinal division. When there are several chromatophores, each daughter-individual receives some and the normal number is restored by subsequent division (see (160)).

In many Diatoms fission of the protoplast commences simultaneously around the whole periphery and gradually extends to the centre, but in *Surirella* (fig. 204 C) it commences at the narrow end of the frustule and gradually advances to the broad end. In the former case silicification and the differentiation of the sculpturing on the valves advance centrifugally. The new connecting-bands are formed after the valves and are apposed to the inner side of the girdle of the old valve. Intercalary bands (p. 573), when present, are formed subsequently between connecting-band and valve and, when several are produced, the new ones are always developed between the valve and the last-formed

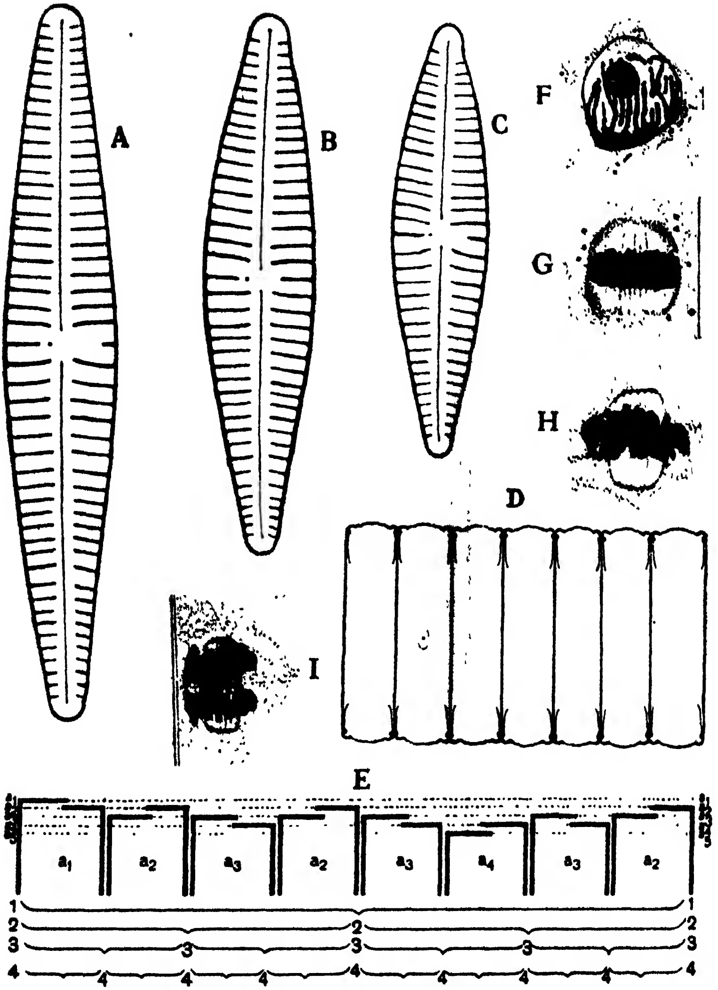

Fig. 205. A–C, *Gomphonema parvulum* (Kütz.) Grun. var. *micropus* (Kütz.) Cl., individuals of a clone derived from an auxospore; A, in April; B, in July; C, in October (same degree of enlargement in all three). D, *Eunotia pectinalsi* (Kütz.) Rabenh. var. *minor* (Kütz.) Rabenh. E, Scheme of division in a colony of *Eunotia*; *1–4* the successive individuals. F–I, *Melosira arenaria* Moore; F, prophase; G, metaphase; H, end of same; I, anaphase. (F–I after Cholnoky; E after Pfitzer from Geitler; the rest after Geitler.)

intercalary band, so that the intercalary band next to the girdle is the oldest. Growth of the girdle in the pervalvar direction is accomplished by the addition of ring-shaped pieces. Except in a few cases all the markings, etc., of the new valve, including the processes met with especially in Centrales, are developed before the two new individuals separate.

The mode of origin of the warts, spines, etc., present in many forms on the outside of the membrane has been a matter of controversy. Müller (150) believed that they were formed with the help of a small quantity of protoplasm remaining between the two new valves, while Schütt (212, 213) denied this and was of the opinion that the cytoplasm in question passed out through the pores which were assumed to occur in the membrane, and formed an extracellular layer (cf. also (219)). The existence of a continuous external protoplasmic layer is, however, improbable in most cases, although Karsten (98) has produced some evidence for its presence in *Planktoniella Sol* (fig. 203 C), where cytoplasm appears to emerge through large marginal pores and to give rise to the characteristic wing. According to Müller the silicified processes, connecting the cells in such a form as *Sceletonema* (fig. 201 D), originate in protoplasmic bridges arising from the intercellular cytoplasm as the new individuals separate; these bridges are supposed to persist so that the protoplasts of successive individuals are connected. Such protoplasmic continuity Müller believed to exist in many colonial Diatoms. It still remains doubtful whether the centrifugally developed outgrowths on the wall of many Centric Diatoms are not formed by the internal cytoplasm, since they are often apparently penetrated by a canal which is probably occupied by cytoplasm. Moreover, the long processes of such forms as *Rhizosolenia* and *Chaetoceras* (fig. 202 B) appear as small prominences long before the new valves are fully differentiated; they exhibit rapid growth in length and probably reach their full size before the valves are completed ((11) p. 90).

CELL-DIVISION AND SIZE

As above mentioned, while one individual at each division is of the same size as the parent, the other is smaller (i.e. narrower) to the extent of the double thickness of a connecting-band.[1] Geitler (57) has recently given a considerable quantity of data as to the rate of decrease in size in cultures. As instances it may be mentioned that single-cell cultures (clones) of *Gomphonema parvulum* var. *micropus*, started with individuals recently produced from auxospores, had in little over two months decreased to about three-quarters and in five months to three-fifths of the original length of the apical axis of the valves (cf. fig. 205 A–C); in the case of *Eunotia formica* a decrease to about

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[1] Cf. (121), (130), (132), (179), (187).

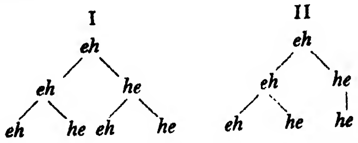
two-thirds took place in five months.[1] In some of the smaller forms division may take place at daily or even shorter intervals, although in the larger ones it is no doubt less frequent.

It is probable that in many cases all the individuals of a given generation divide with approximately equal frequency, so that if a population derived from a single parent-individual is measured the average size is the arithmetic mean between the largest and smallest individuals. If the successive individuals of decreasing size are indicated by the letters of the alphabet, we have:

	a	*b*	*c*	*d*	*e*	*f*
Parent-cell	1	—	—	—	—	—
1st generation	1	1	—	—	—	—
2nd ,,	1	2	1	—	—	—
3rd ,,	1	3	3	1	—	—
4th ,,	1	4	6	4	1	—
5th ,,	1	5	10	10	5	1

This is known as the binomial law. It will be noted that, as division continues, the average size of the population shifts progressively to smaller and smaller dimensions. This method of division has been demonstrated for *Nitzschia linearis* by Miquel (131), while Hustedt (86) has established it for *Eunotia didyma* var. *elegantula* and *Achnanthes brevipes* by a study of the individuals composing the colonies (cf. also (57) and fig. 205 E).

In such ribbon-shaped colonies, which must of course have originated from a single individual, the sequence of division can be recognised from the characteristic relation of the two valves of an individual. If all individuals divide with equal frequency, we shall always find the hypothecae of adjacent frustules in contact, as in the case of the species just mentioned (fig. 205 E). If, however, only one of the two individuals of any generation divides we shall find that at certain points adjacent individuals have epitheca and hypotheca in contact. If *e* represent epitheca and *h* hypotheca, the two methods of division are indicated by the following schemes:



It will be noticed that the individuals at the extremities of such colonies will always have the epithecae facing outwards. In this way Müller (140) was able to establish that in *Melosira arenaria* the second method of division obtains, the larger daughter-individuals of any generation

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[1] It is probable that in nature, owing to a less rapid rate of division, the decrease in size would be slower.

dividing more frequently than the smaller ones, which give rise to daughter-individuals only at every alternate division period. By this means the rate of decrease in size is slowed down and Hustedt ((87) p. 100) suggests that such a condition may occur especially in thick-walled forms where the rate of decrease in size of the smaller individuals is of course particularly rapid. To judge by Geitler's work (57), however, such cases are probably the exception.

The normal rate of decrease in size is somewhat slowed down by the fact that the thickness of all parts of the wall (including the connecting-bands) decreases with the size of the individual ((57) p. 12, (130)). The change in dimensions is almost entirely due to shortening of the apical axis, the transapical one exhibiting in proportion a much smaller decrease and sometimes scarcely any at all, while the pervalvar axis decreases but slightly and often remains practically constant (cf. also (223)).[1] These facts altogether disprove the existence of any marked capacity of the valves to enlarge such as has been assumed by some investigators (59, 61). In view of the rigidity imposed by the always mature epitheca of the new individual, it is indeed difficult to conceive how this could occur. Where silicification is slight, there may be some enlargement by intussusception, as perhaps occurs in *Nitzschia Closterium* forma *minutissima* where pure cultures extending over two years showed no marked reduction in size (1 *a*). But for the vast majority of Diatoms such growth is no doubt altogether impossible (cf. (20), (86) p. 67). Geitler ((57) p. 86) has drawn attention to the fact that in *Eunotia pectinalis* var. *minor* (fig. 205 D) the connecting-bands have an arched contour so that the new valves formed during division are as large as those of the parent, with the result that there is no decrease in size. This case at present stands isolated.

The reduction in size of a population is compensated sooner or later by the formation of so-called *auxospores*, a process in which the protoplast escapes from its rigid envelope and during which a return to maximum dimensions is rendered possible (131). Geitler (57) has shown clearly that in Pennate Diatoms auxospore-formation only takes place when the individuals have reached a certain reduced size ($8 \cdot 5\,\mu$ in *Navicula seminulum*), and that below a certain minimum ($5 \cdot 5\,\mu$ in the case cited) it likewise fails to occur; such small individuals continue to divide until a limit is reached, the ultimate generations often showing various abnormalities and simply perishing. It is significant in this connection that in the above-mentioned species of *Eunotia* with cells of constant dimensions no auxospores have been observed. Among Centric Diatoms, too, formation of auxospores

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[1] According to Richter (187) this is not the case in *Nitzschia putrida*, the pervalvar axis lengthening as the apical one shortens, so that the volume remains constant. This is, however, very doubtful (cf. (57) p. 183).

only takes place in individuals of a certain range of size.[1] It must, however, be emphasised that decrease in size is not likely to be the only factor conditioning auxospore-formation, especially in the numerous cases among Pennate Diatoms in which a sexual fusion is involved. The factors are no doubt in part environmental, as in the similar reproductive processes of other Algae ((32) p. 100, (57), (130) p. 521, (132) pp. 84, 174). It seems, however, that these forms do not reach the state (tonus) admitting of auxospore-production until a certain size has been reached.

In nature the formation of auxospores is comparatively rare, and it is owing to this fact that various authorities have felt compelled to assume a power of enlargement on the part of the individual diatom. It must, however, be realised that the rate of decrease in size is comparatively slow and for *Synedra ulna* Hustedt ((86) p. 68) calculates that more than 1000 divisions would be necessary to reduce the size from the maximum to the minimum, a number hardly likely to occur during a single period of vegetative activity. According to Skabitschewsky (220) four to five years elapse between two periods of auxospore-formation in *Melosira baicalensis*. Nipkow (157), examining the successive sediments in Swiss lakes, found that there is a gradual decrease in size spread over a number of years (two to five in the case of *Stephanodiscus Hantzschii*, four in *Tabellaria fenestrata*), followed by a brief phase of auxospore-formation. *Fragilaria crotonensis* only showed auxospore-formation three times in 18 years. In *Melosira islandica* var. *helvetica*, on the other hand, the latter process occurred at frequent intervals. Like other investigators Nipkow noted abundant division in the first period succeeding auxospore-formation. Karsten ((91) p. 53) comments on the frequent almost total disappearance of a diatom-population after auxospores have been formed.

AUXOSPORE-FORMATION IN CENTRALES

The production of auxospores in Centric Diatoms is a comparatively simple process and is not dependent on any association of individuals in sexual reproduction, consisting essentially in a rejuvenescence of the protoplast. The two halves of the wall are thrust apart by the protoplast which becomes enveloped in a thin, slightly silicified pectic membrane, the *perizonium*, within which the protoplast undergoes a rapid enlargement (cf. fig. 206 F). Sooner or later valves and connecting-bands are secreted internal to the perizonium and a new individual, more or less appreciably larger than the parent, is produced; the valves of the new individual are formed successively (cf. fig. 206 B, C). According to Liebisch ((118) p. 60) the perizonium in these forms is constituted merely by the stretched pectic layer of the membrane of the parent-cell.

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[1] See (15), (200), (224), (226); cf. however (220).

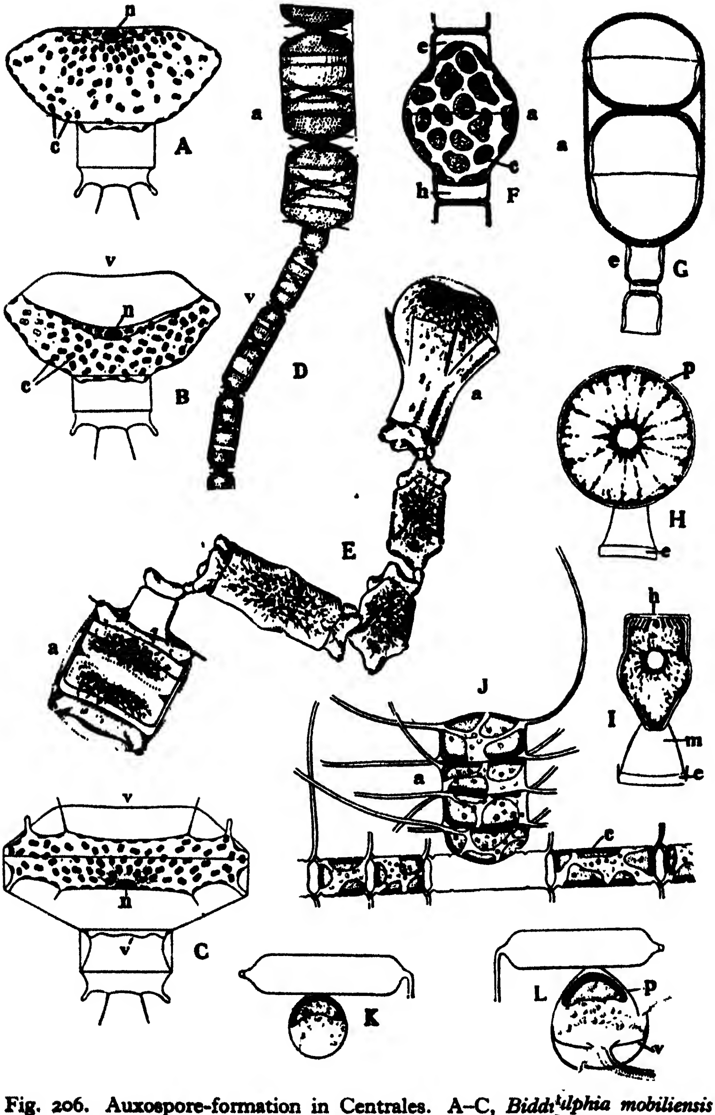

Fig. 206. Auxospore-formation in Centrales. A–C, *Biddulphia mobiliensis* Bail.; A, escape of protoplast; B, secretion of first and C, of second valve. D, *Melosira nummuloides* (Dillw.) C. Ag., thread before (*v*) and after (*a*) auxospore-formation. E, *Triceratium antediluvianum* (Ehrenb.) Grun., with two auxospores. F, *Melosira varians* Ag. G, *M. Jürgensii* Ag., auxospore

The process is very simple in *Melosira* ((92) p. 213, (154), (159), (191)). In *M. varians*, in which auxospore-formation is comparatively frequent, and in *M. Jürgensii*(76) the spore occupies part of the epitheca of the parent-individual, whilst the opposite rounded end projects into the hypotheca (fig. 206 F, G, *a*). In other species of the genus (e.g. *M. nummuloides*), however, the auxospore lies altogether outside the thecae of the parent (fig. 206 D). The new individuals produced from the auxospores commonly remain within the continuity of the parent-thread, but in *M. Jürgensii*, for example, the hypotheca and the rest of the attached thread falls off, so that the auxospore is terminal (fig. 206 G). In some species (e.g. *M. arenaria*) the pervalvar axis of the auxospore is inclined to the valvar plane of the parent-individual (76, 220).

The process of production of auxospores was studied fully in *Biddulphia mobiliensis* by Bergon(14). Here division of the cell immediately precedes the formation of auxospores, the two daughter-protoplasts without producing new valves escaping from those of the parent (fig. 206 A) and forming a pair of spores. The latter of course fall apart, but remain clinging to the respective valves of the parent-cell (fig. 206 A–C). The nucleus (*n*) at first lies adjacent to the outer face of the spore (fig. 206 A, B) where the first valve (*v*) is secreted; later it wanders to the inner face (fig. 206 C) and this is followed by the formation of the second valve (*v′*).

In many Centrales the long axes of parent-individuals and auxospores coincide, but in some species of *Chaetoceras* (e.g. *C. cochlea*) the auxospore arises laterally on the parent-cell (fig. 206 K, L) and the new colony produced from it stands at right angles (fig. 206 J) to the long axis of the parent(88, 170, 208). The epitheca of the first cell adjoining the parent in such cases lacks the pair of long horns, typical for the *Chaetoceras*-valve. A similar lateral formation of auxospores takes place in some species of *Rhizosolenia*(209).

Among the numerous special cases mention may be made of *Arachnoidiscus Ehrenbergii*(236), an epiphyte attached by the epitheca. Here the protoplast covered by the hypotheca is gradually raised aloft by the secretion of a mucilage-stalk (fig. 206 I) at the end of which the auxospore is formed after the protoplast has withdrawn from the hypotheca (fig. 207 H). In *Triceratium* (*Amphitetras*) *antediluvianum*

once divided. H, I, *Arachnoidiscus Ehrenbergii* Bailey; H, young auxospore; I, escape of protoplast carrying up hypotheca (*h*). J, *Chaetoceras medium* Schütt, product of auxospore (*a*) formed perpendicular to main thread. K, L, *C. cochlea* Schütt; K, auxospore; L, formation of first valve. *a*, auxospore; *c*, chromatophore; *e*, epitheca; *h*, hypotheca; *m*, mucilage-stalk; *n*, nucleus; *p*, perizonium; *v*, *v′*, valves. (A–C after Bergon; D after W. Smith; E after Liebisch; F after West; G after Hustedt; H, I after Yendo; the rest after Schütt.)

(117), a cosmopolitan marine form, a great elongation of the connecting-bands takes place prior to spore-formation and the girdle is later ruptured irregularly by the enlarging auxospore (fig. 206 E).[1]

As regards the increase in size brought about by the formation of auxospores in Centric Diatoms, Müller (154) gives the relative dimensions of spores and parent-cells as 1 : 2–2·6 for *Melosira islandica* and 1 : 3·4–4 for *M. italica*, the last probably representing the maximum increase that will be found to occur (cf. also (220)).

Karsten (92) found that the nuclei of the young auxospores in *Melosira nummuloides* contained two nucleoli, whereas in the vegetative cells there was only one, although Geitler ((57) p. 201) was unable to confirm this. Karsten interpreted his observation as indicating a suppressed nuclear division during the formation of the auxospores in *Melosira* and believed he found similar evidence in *Sceletonema* ((92) p. 218). Recently various cases of nuclear division during auxospore-formation in Centrales have been reported. Thus, in the young auxospores of *Melosira arenaria*, Cholnoky (33 *b*) records the presence of three nuclei, one larger than the other two which gradually degenerate (fig. 214 D, E). The single large nucleus is regarded as possibly representing a fusion-product. Persidsky (176) has likewise shown that the young auxospores of *Chaetoceras* contain four nuclei (fig. 214 I) and believes he has established that they are formed meiotically. The possibility of a reduction division and of subsequent autogamy cannot be denied, but further research will be necessary to substantiate this clearly (cf. also p. 637).

AUXOSPORE-FORMATION IN PENNALES

Karsten (100, 101) regards the process of auxospore-formation in the Tabellariaceae (Fragilarioideae) as the simplest among the Pennales and believes that it establishes a definite point of contact with the formation of auxospores in the Centrales. Geitler ((57) p. 200), on the other hand, regards it as a derived process and possibly apogamous. In *Rhabdonema arcuatum* (94, 120, 222) an older cell provided with numerous intercalary bands undergoes division without formation of new valves on the part of the daughter-protoplasts (cf. *Biddulphia mobiliensis* and fig. 207 A). The latter secrete abundant mucilage (*m*), whereby the two thecae are pushed apart, and within this envelope each enlarges in a direction perpendicular to the long axis of the parent-cell (fig. 207 B) and secretes a perizonium (*p*).

In *Rhabdonema adriaticum* ((94) p. 32, (116)) the hypotheca of an auxospore-forming frustule (fig. 207 C, D) rapidly secretes numerous intercalary bands (*i'*), differing from those of the normal individuals (*i*)

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[1] For other literature on auxospore-formation in Centrales, see (2), (15), (74), (98), (125), (129), (130), (167–169), (205), (206).

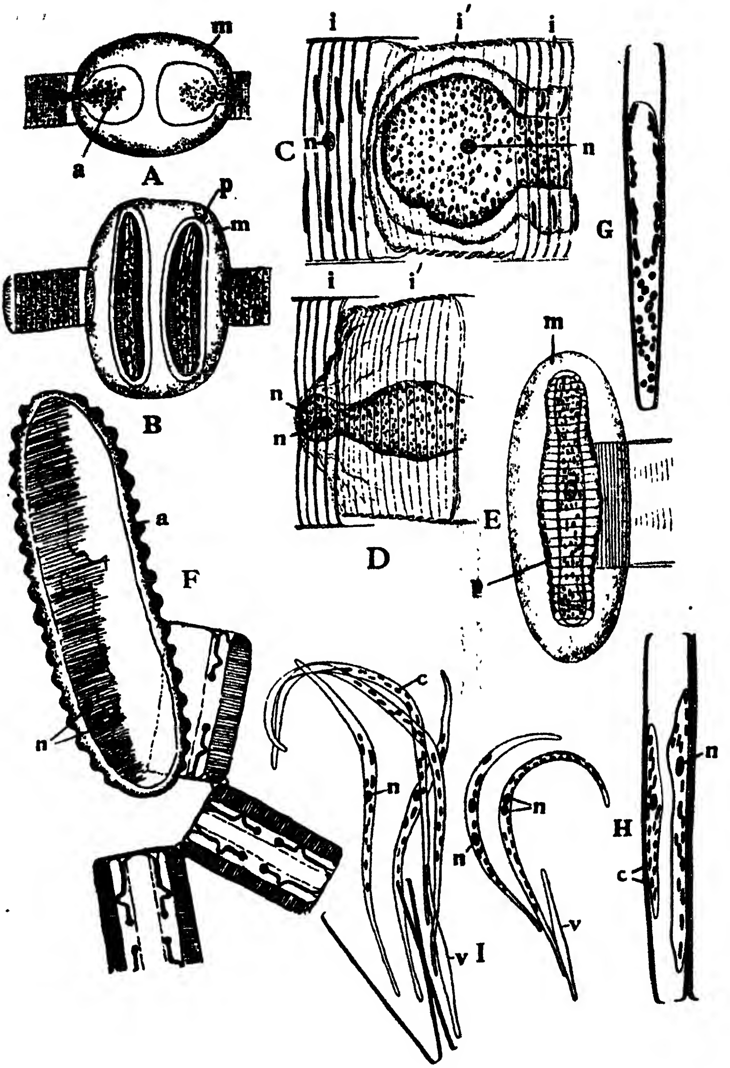

Fig. 207. Auxospore-formation in Fragilarioideae (all after Karsten). A, B, *Rhabdonema arcuatum* (Lyngb.) Kütz.; B with mature auxospores. C–E, *R. adriaticum* Kütz.; C, D, formation of accessory intercalary bands (*i′*); in D protoplast with two nuclei, in C one of these extruded; E, mature auxospore. F, *Grammatophora marina* (Lyngb.) Kütz., auxospore. G–I, *Synedra affinis* Kütz.; G, H, two successive stages, in H with divided protoplast; I, germinating auxospores. *a*, auxospore; *c*, chromatophores; *i*, *i′*, intercalary bands; *m*, mucilage; *n*, nucleus; *p*, perizonium; *v*, valve.

in the lack of sculpturing and the absence of ingrowing septa (p. 575); as a result the hypotheca within which the protoplasm accumulates becomes widely removed from the epitheca. The nucleus now divides, the two resulting nuclei being unequal in size (fig. 207 D). The smaller of the two is gradually extruded from the protoplast (fig. 207 C) which then escapes within an envelope of mucilage inside which the perizonium is secreted (fig. 207 E). In this case therefore only one auxospore is formed, although the division of the nucleus into two perhaps indicates a derivation from the type found in the other species.

In *Grammatophora* (100, 116) the process is very similar, but nuclear division only occurs after escape of the protoplast, and in later stages the two nuclei are found close together (fig. 207 F). Karsten assumes that they subsequently fuse, but for this there is no evidence and it is equally possible that one subsequently degenerates. The auxospore adheres to one valve with the help of mucilage, but there is in this case no complete gelatinous envelope. In all the investigated Tabellariaceae there is thus a nuclear division associated with auxospore-formation, although it is only in *Rhabdonema arcuatum* that this leads to the production of two spores.

Synedra affinis, the only species of the genus in which auxospore-formation has yet been certainly recorded, like *Rhabdonema arcuatum* produces two auxospores from a single individual after division of the protoplast (fig. 207 G, H). Karsten ((91) p. 33, (101) p. 192) observed that during the subsequent elongation of the young auxospores (fig. 207 I) a nuclear division occurred, although the resulting nuclei soon fused again, and he regarded this as a case of autogamy (cf. p. 631). The evidence for nuclear fusion is, however, unsatisfactory.

In other families of Pennales auxospores generally result from a union of naked amoeboid protoplasts derived from distinct individuals, a method that is only readily possible in forms endowed with the power of movement. It has been established in various cases that the ordinary individual is diploid and that reduction-division occurs during the formation of gametes, and it is more than probable that this is true of all Pennales. Many variants of the process of auxospore-formation have, however, come to light (52, 87, 103, 104, 125).

In many of the Biraphideae (except Surirelloideae) each of the conjugating individuals furnishes a pair of gametes and two auxospores result from the sexual fusion. This method was first fully studied by Klebahn (104) in *Rhopalodia gibba* (cf. also (222)). Here two individuals, often of unequal size, become apposed by their ventral girdles (fig. 208 A), being united by pads of mucilage (*m*) secreted at the poles, while the contracting protoplasts secrete mucilage leading to a gradual separation of the halves of the frustules (cf. fig. 208 B). In each protoplast two successive nuclear divisions (fig. 208 B, F) ensue

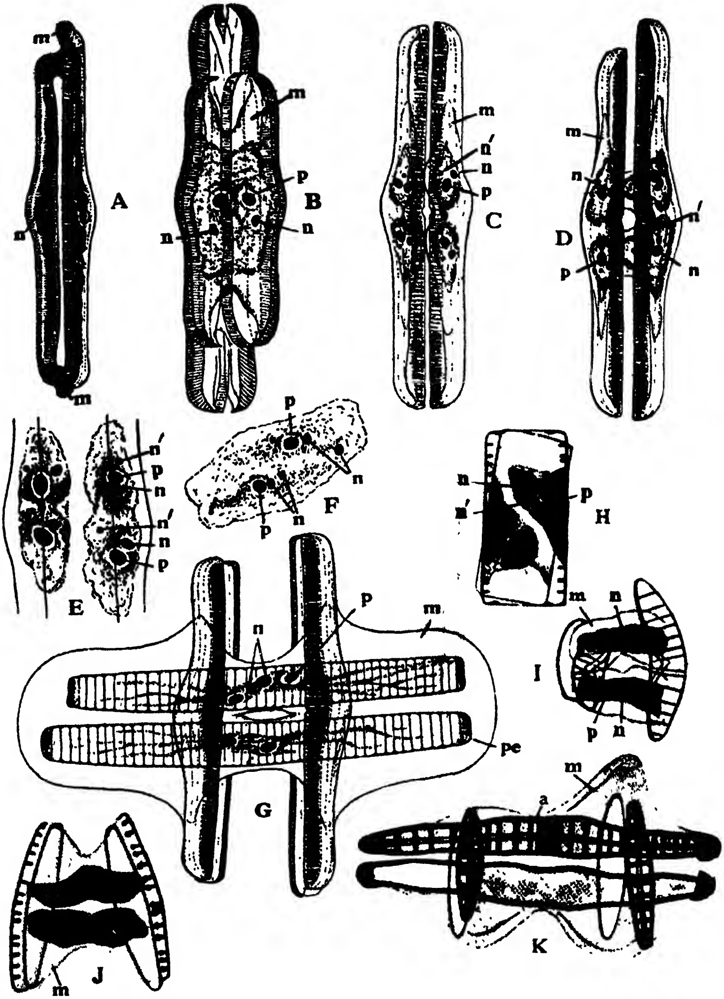

Fig. 208. Auxospore-formation in Pennales (two spores from two parent-individuals). A–G, *Rhopalodia gibba* (Ehrenb.) O. Müll., in B the girdle-view, in the others the valve-view; A, approximation of frustules; B, separation of girdle-bands, contraction of protoplasts, two nuclei; C, division into gametes, abortion of one nucleus in each; D, fusion; E, protoplasts of the two individuals at a stage between that in B and C; F, one protoplast at a stage slightly later than B; G, mature auxospores. H, I, *Epithemia zebra* (Ehrenb.) Kütz. var. *saxonica* (Kütz.) Grun.; H, the two copulating individuals in girdle-view, with divided protoplasts; I, fusion, parent-cells in valve-view. J, K, *Denticula Vanheurcki* Brun; J, fusion; K, mature auxospores. *a*, auxospore; *m*, mucilage; *n*, *n′*, nuclei; *p*, pyrenoids; *pe*, perizonium. (A–G after Klebahn; the rest after Geitler.)

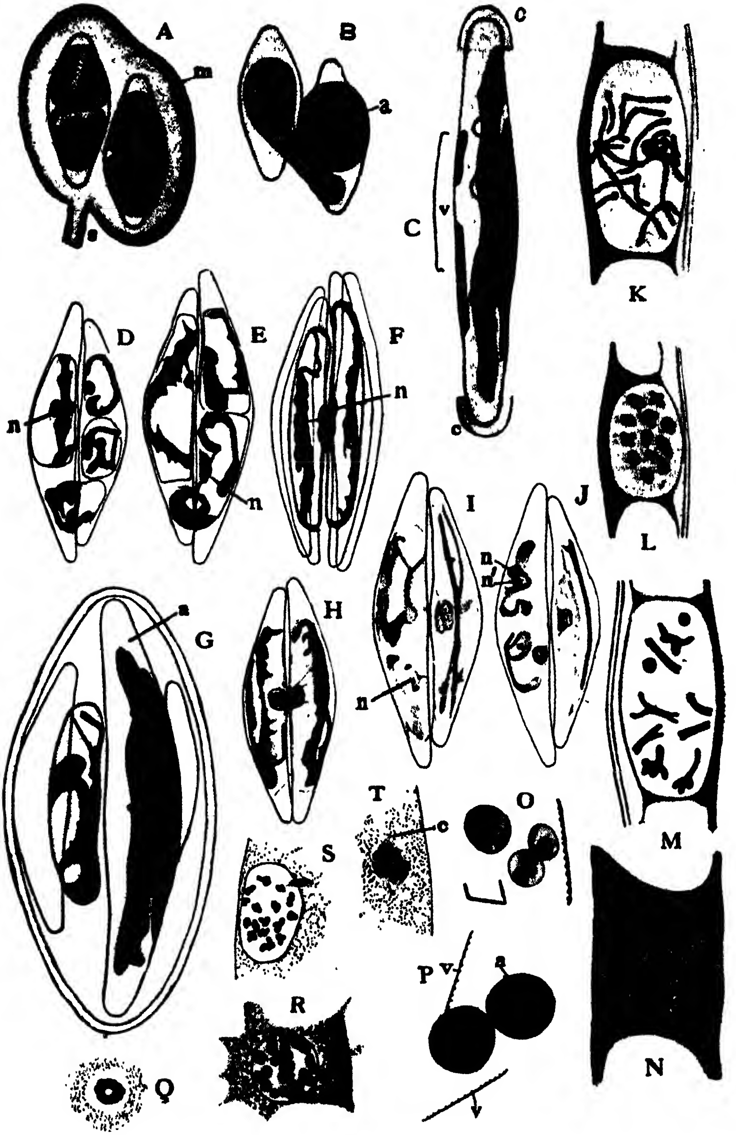

Fig. 209. Auxospore-formation in Pennales (two spores from two parent-individuals). A–C, *Gomphonema parvulum* var. *micropus* (Kütz.) Cl.; A,

which presumably bring about reduction, after which two of the resulting nuclei (fig. 208 C, E, *n'*) gradually diminish in size. Each protoplast now divides into two, the division-products later lying one in front of the other along the apical axis (fig. 208 C). The mucilage-envelope then becomes protruded opposite each half-protoplast (fig. 208 C), and within the gelatinous bridges thus formed the undifferentiated gametes from the respective individuals fuse in pairs (fig. 208 D) to form two zygotes which lie between the two parent-individuals. The small nuclei soon disintegrate completely, whilst fusion of the larger ones is delayed for some little time. The zygotes elongate markedly perpendicular to the apical axis of the parent-cells to form the auxospores and each becomes enveloped by a perizonium (fig. 208 G).

Essentially the same method of auxospore-formation has been observed in *Amphora* ((57) p. 205, (118) p. 37), *Epithemia* (222) (fig. 208 H, I), and *Denticula* ((57) p. 165) (fig. 208 J, K). In all these cases the behaviour of the two gametes is identical even though they be of unequal size, as easily happens if one parent-individual is larger than the other. The resulting auxospores in such isogamous fusions are always elongated at right angles to the apical axis of the parent-individuals (fig. 208 G, K).

Quite commonly, however, the process of sexual fusion is anisogamous, one of the two gametes formed by a conjugating individual being passive, while the other is active. A zygote is therefore produced within each parent-individual (fig. 210) and, according to Geitler (57), this method invariably results in two auxospores whose long axis is parallel to that of the parents. Auxospore-formation of this kind is probably widespread in *Navicula* (91, 94), is recorded for *Nitzschia subtilis* (51), and has been fully described by Geitler in *Cymbella lanceolata* (49) and *Gomphonema parvulum* var. *micropus* ((57) p. 54). The two copulating individuals are usually surrounded by a wide envelope of secreted mucilage.

association of individuals; B, passage of right-hand to left-hand gamete, the right-hand individual with a zygote (*a*); C, mature auxospore with the polar caps (*c*), on the left a valve (*v*) of one of the parents. D–N, *Cymbella lanceolata* (Ehrenb.) Van Heurck; D, gamete from cell on left passing over into the right-hand cell; E, fusion of one pair of gametes; F, the two zygotes; G, auxospores, that on the left not fully developed; H–J, nuclear divisions in the two copulating cells, H shows the first, I, the second division, and J, the abortion of two of the four nuclei; K–N, stages in meiosis. O, P, *Nitzschia fonticola* Grun.; O, a zygote on the left, two gametes on the right; P, pair of mature zygotes. Q, R, *Gomphonema geminatum* Ag.; Q, metaphase of heterotype division; R, diakinesis. S, T, *Cymbella cistula* (Hempr.) Grun., meiosis; S, diakinesis; T, anaphase. *a*, auxospore or zygote; *c*, centrosome; *m*, mucilage; *n*, *n'*, nucleus; *s* (in A), mucilage-stalk; *v*, valve. (Q, R after Meyer; S, T after Cholnoky; the rest after Geitler.)

In the case of *Gomphonema* (cf. also (128)) (fig. 209 A) the mucilage-envelope is attached by a mucilage-stalk (*s*) to the substratum, so that one individual appears to seek out the other which remains adhering to its stalk; moreover the two frustules are here always inverted with respect to one another, the apical end of the one being next to the basal end of the other (fig. 209 A). Division of the protoplasts ensues, after the two nuclear divisions bringing about reduction have occurred, and always takes place along the valvar plane, i.e. the one along which vegetative division occurs. Subsequently, however, the two half-protoplasts alter their position, coming to lie one in front of the other along the apical axis (fig. 209 A). It is probable that this applies to all forms in which two gametes are produced per parent-individual (cf. also (91)).

Conjugation takes place successively between the gametes of the two individuals, one gamete first passing from *a* to *b*, whereupon the other gamete of *b* passes over to *a* (cf. figs. 209 D, E, and 210); in *Gomphonema* the conjugation is crosswise, as the figures show. In *Anomoeoneis sculpta* (28) and *Cymbella lanceolata* (49) a difference of size between the two gametes produced by an individual has been observed (cf. fig. 209 D, E), and it has been stated that the smaller is the active one. More recently, however, Geitler (57) denies that there are any constant differences in size between active and passive gametes. Quite commonly the two conjugating individuals are of unequal dimensions, in which case the small gametes of the one function respectively as active and passive gametes.

Geitler is, moreover, of the opinion that the anisogamy in all these forms is only apparent and that it results from the fact that one gamete matures earlier than the other and that copulation takes place within the confines of a relatively tough mucilage-envelope. Where the latter is softer (*Nitzschia fonticola* (57) p. 170; *Achnanthes longipes* (91) p. 43) the zygotes show no regularity in their position and moreover are characteristically spherical (fig. 209 O, P) by contrast to their elongate form in the other case. The conclusion that it is not a sexual differentiation that is responsible for the apparent anisogamy does away with the necessity of assuming the existence of a bisexual condition in the conjugating individuals (cf. also (32) p. 101) for, if there were sexual differentiation, one gamete of an individual would be male and the other female, and it would further be necessary to assume self-sterility to account for the absence of conjugation between the two gametes belonging to the same individual.

In a limited number of cases each conjugating individual produces only one gamete, the zygote lying either between the two parents (fig. 211 O) or within one of them (fig. 211 J, Q); in the latter case we probably have true physiological anisogamy and in *Cocconeis placentula* var. *pseudolineata* (47, 57) this is generally combined with morphological anisogamy, the individual furnishing the active gamete being usually smaller than the other (fig. 211 P). The sexes in such cases are not, however, genotypically determined (cf. p. 44), since individuals of a clone will always copulate; it may be that sexual differentiation already exists when the individuals come together or it may only arise during the reduction-division. Isogamy is known in *Surirella* (95, 99) (fig. 211 A–C), *Achnanthes flexella* ((231) p. 269), *Rhoicosphenia curvata* (26), *Eunotia* ((57) p. 72, (222)), and certain varieties of *Cocconeis placentula* (47) (fig. 211 N, O), as well as in *C. pediculus* (47, 120). Anisogamy occurs in the above-mentioned variety of *Cocconeis placentula* and in *Navicula seminulum* ((57) p. 38) (fig. 211 H–K), so far the only member of the genus known to produce a single gamete from each conjugating individual. The general character of the process of conjugation in these cases should be sufficiently clear from a perusal of fig. 211.

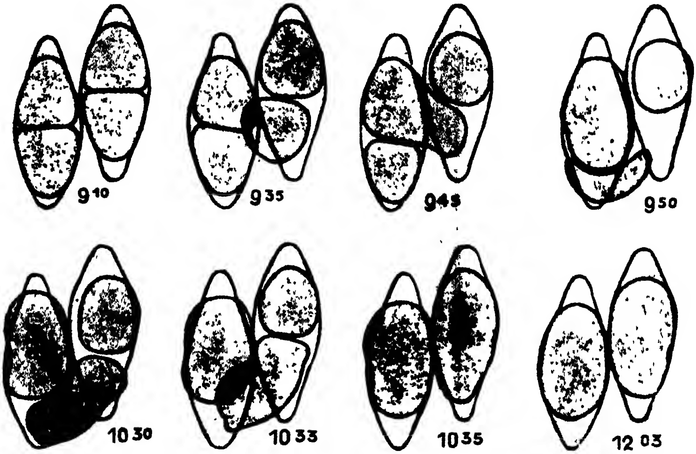

Fig. 210. *Gomphonema parvulum* Grun. var. *micropus* Cl., diagrammatic representation of the course of sexual fusion (after Geitler).

Certain general features of the conjugation-process remain to be considered. In the vast majority of cases the conjugating individuals become apposed by their girdles within an envelope of mucilage which according to Liebisch (118) is merely the swollen pectin-membrane of the parent-individuals (cf. also (57) p. 209). According to Cholnoky (31, 32) it is of a different nature to that formed for attachment, etc., by vegetative individuals. In some cases, however, the mucilage merely forms a narrow conjugation-canal, as in *Nitzschia subtilis* (51, 55), where

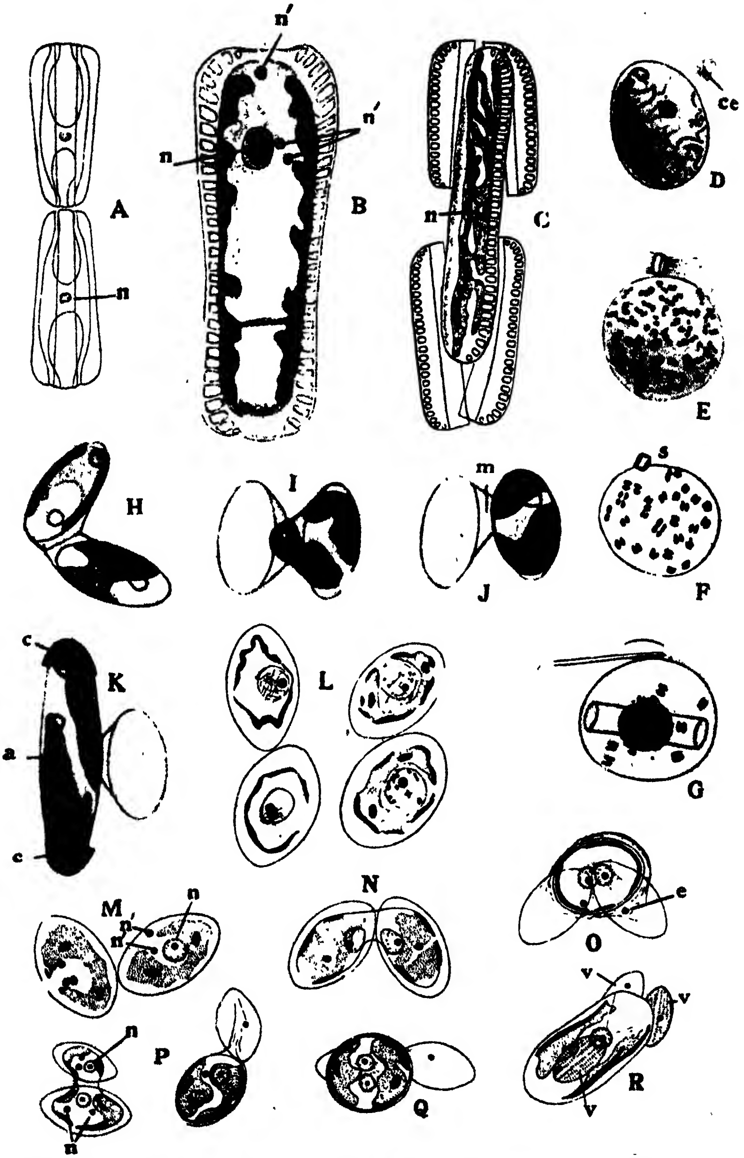

Fig. 211. Auxospore-formation in Pennales (one spore from two parent-individuals). A–G, *Surirella splendida* Kütz., A–C, conjugation; D–G,

the mucilage-envelope is lacking, and occasionally in *Cocconeis placentula* ((47) p. 527, (95)) (fig. 211 N). In *Surirella* (95) the two individuals become apposed by their narrow ends being joined by a cushion of secreted mucilage (fig. 211 A). In various cases (31) the two conjugating individuals have been shown to be sister-cells (so-called *pedogamy*), but this is certainly not the rule. In stalked forms like *Gomphonema* and *Rhoicosphenia* one of the two individuals is often devoid of a stalk and has clearly approached the other by active movement (cf. also (91)). In the case of *Rhoicosphenia*, Cholnoky (26) states that the two conjugating individuals are either sisters or one (regarded as male) wanders into the mucilage-envelope of the other (the female). Where one or two large chromatophores are present the commencement of the process of auxospore-formation is often marked by a movement of the former from the girdle onto the valve-faces (91). According to Geitler ((57) p. 209, also (32)) isogamous fusion takes place slowly, whereas in cases of anisogamy it is very rapid, often only occupying a few minutes (cf. fig. 210). In various cases Karsten (91) records a fusion of chromatophores and pyrenoids in the zygotes.

Meiotic division of the nucleus has been definitely observed in *Surirella splendida* (*S. saxonica* (99), fig. 211 D–G), *Nitzschia subtilis* (51), *Cymbella lanceolata* ((49), fig. 209 K–N), *C. cistula* ((33), (108), fig. 209 S, T), *Gomphonema geminatum* ((128), fig. 209 Q, R), *Cocconeis placentula* ((47), fig. 211 L), and *Rhoicosphenia curvata* (26), while occasional data indicating meiosis have been recorded in a considerable number of other forms. A particularly detailed study of the process has been undertaken by Geitler (49) and Cholnoky (33). In all, except *Rhoicosphenia* where only the heterotype was observed, two successive nuclear divisions have been recorded, two or three of the resulting nuclei, according as two gametes or only one are formed, gradually aborting (fig. 211 B, M, P) or being eliminated. In *Cocconeis*, however, only one of the two nuclei formed at the first division survives and divides again (57). Where two gametes are produced from each individual the persisting nuclei are derived from one of each of the nuclei formed at the first division (heterotype) (cf. however (28)).

meiosis; B, the four nuclei in one of the conjugating individuals; C, auxospore; D, synapsis; E, shortening of chromosomes, formation of spindle; F, diakinesis, penetration of spindle into nuclear cavity; G, chromosomes aggregating on spindle. H–K, *Navicula seminulum* Grun.; I, fusion nearly complete; J, zygote; K, auxospore with polar caps (*c*). L–O, *Cocconeis placentula* Ehrenb. var. *klinoraphis* Geitl.; L, early stage of conjugation, nuclei on left in synapsis, on right diakinesis; M, the same, right-hand individual with one large and two small nuclei; N, fusion; O, young auxospore. P–R, *C. placentula* var. *pseudolineata* Geitl.; P, fusion; Q, zygote; R, auxospore, with three valves of the parents. *a*, auxospore; *ce*, centrosome; *e*, extruded nucleus; *m*, mucilage; *n*, *n'*, nuclei; *s*, spindle; *v*, valve. (A–G after Karsten; the rest after Geitler.)

The supernumerary nuclei do not in all cases degenerate, one of those formed at the first division being sometimes extruded with a small quantity of cytoplasm (e.g. *Cocconeis*, figs. 211 O, 212 A, *e*, *Navicula seminulum*).[1] Geitler (57) no doubt rightly regards the extruded nucleus as an abortive gamete, the formation of two gametes per individual being regarded as probably primitive. Moreover, in some cases one or other of the supernumerary nuclei fails to degenerate and is to be found within the mature auxospore; thus, Meyer (128) in *Gomphonema geminatum* occasionally found zygotes with three equal nuclei. A similar condition observed by Geitler ((47) p. 535) in *Cocconeis placentula* var. *klinoraphis* is due to the occasional conjugation of three individuals. The fate of such triploid zygotes has not been established (cf. also (95)).

The products of fusion in all cases become enveloped in a membrane and possibly as a general rule pass through a brief resting period ((26), (31), (57) p. 210) before the enlargement to form the auxospores commences. When this happens, the zygote membrane is in the majority of cases ruptured and remains as two polar caps at the ends of the auxospore (figs. 208 K, 209 C, 211 K, *c*) or more rarely undergoes gelatinisation. In these cases the perizonium is a new membrane. It seems, however, that the zygote-membrane sometimes persists and gradually enlarges to form the perizonium. As a rule the latter probably undergoes silicification when it has reached its full size and, though commonly smooth, may exhibit transverse markings similar to those of the ordinary individuals (fig. 208 G, K).

In *Rhoicosphenia* Cholnoky (26) describes division of the contents of the zygote to form two auxospores, but Karsten (102) considers that his figures are open to the interpretation that conjugation in this genus takes place either between single gametes or between pairs of gametes, one or two auxospores being produced. In *Cocconeis* (47) the auxospore is raised well above the substratum on a mucilaginous stalk (fig. 212 A). Liebisch ((118) p. 58) points out certain resemblances between auxospore-formation and the craticular stages above discussed (p. 575).

The secretion of the valves of the new individual, after the enlargement of the auxospore is completed, invariably takes place successively (figs. 211 C, 212 B), the epitheca being probably in all cases formed first (also in Centrales); frequently this formation of valves is combined with movement of the nucleus first to one face and then to the other. Geitler ((57) p. 211) draws attention to the fact that the first valve develops no connecting-band and that this valve is usually arched, so that the first individual (often also called an auxospore) is asymmetric in girdle-view (fig. 212 C, D). The next division thus affords two individuals of unequal width (fig. 212 E). The characteristic markings of the species are often only realised after a number of generations.

[1] Cf. the case of *Rhabdonema adriaticum*, described on p. 622.

Autogamy is probable in a few cases, but in none of these are the data quite adequate. In *Achnanthes subsessilis* Kütz. ((94) p. 43) there is no approximation of individuals, but the protoplast divides into two uninucleate portions (fig. 212 F). In later stages Karsten found only a single protoplast with double the number of chromatophores and approximated nuclei, presumably about to fuse (fig. 212 G). In *Amphora Normani* (53) the auxospore is likewise formed by a single individual, the process commencing with a division of the single chromatophore and of the nucleus (fig. 212 H), the two nuclei later fusing within the enlarging spore without a segregation of the protoplasts having taken place (fig. 212 I, J). A second nuclear division was not observed in either of these cases, but Geitler ((57) p. 198) considers it probable that it has been overlooked (cf. also the case of *Synedra* discussed on p. 622).

A considerable number of examples of apogamy have come to light. In *Surirella gemma* ((101), (118) p. 45) two individuals enveloped in mucilage each form an independent auxospore and the same occurs in *Cymatopleura* (95),[1] *Libellus constrictus* (90),[2] and some species of *Cymbella* (197). There is, however, not always an approximation of individuals. In *Cocconeis placentula* var. *lineata* (47) such approximation usually occurs (fig. 212 K, L), but not invariably; in this case Geitler was able to show that there is no reduction of chromosomes, although there are two nuclear divisions and the first shows a distinct synapsis and diakinesis stage (fig. 212 K, M). West ((231) p. 269) recorded the formation of auxospores from single individuals enveloped in mucilage in *Navicula amphisbaena* (fig. 212 N) and *Pinnularia viridis* (fig. 212 O), the protoplast swelling up and escaping as the single spore. This authority was of the opinion that production of auxospores without conjugation was much the commonest method among Pennales, but recent investigations with their abundant records of the occurrence of a sexual fusion appear to indicate that the former condition is rather to be regarded as the exception. It is not impossible too that the cases of apparent apogamy in the two species just mentioned, which are merely based on casual observations, will prove on reinvestigation to be of a different nature (autogamy?). In *Bacillaria paradoxa*, Karsten (94, 101) failed to find any evidence of nuclear division in the formation of the auxospore from the single individual.

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[1] Pfitzer ((179) p. 119), however, recorded sexual fusion in *Cymatopleura solea*, one of the species in which Karsten describes apogamy.

[2] Cf. however (57) p. 198.

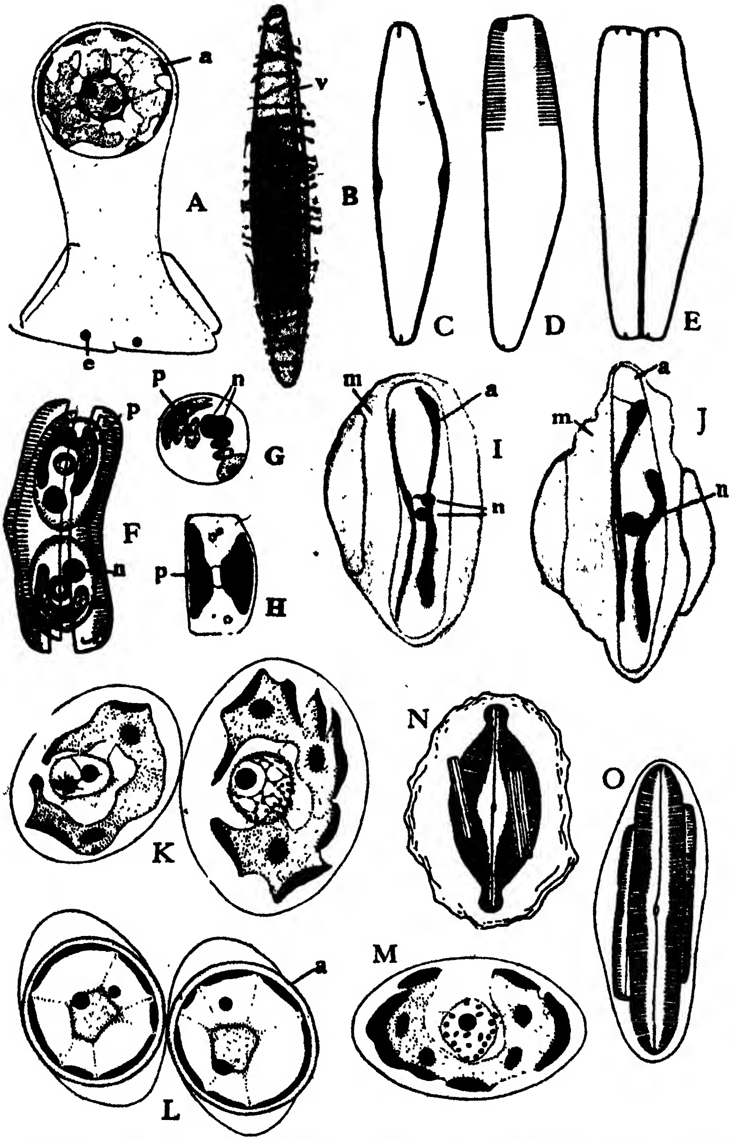

Fig. 212. A, *Cocconeis placentula* Ehrenb. var. *klinoraphis* Geitl., young auxospore with fusion nucleus and extruded nuclei (*e*) at the base of the stalk.

THE MICROSPORES OF CENTRALES

These structures were first recorded by Murray (155) in 1896, who observed within the cells of *Coscinodiscus concinnus* and of species of *Chaetoceras* a number of rounded protoplasmic masses in multiples of two which he interpreted as reproductive cells. Gran in 1902 (65) recorded similar bodies in *Rhizosolenia styliformis* and in 1904 ((66) p. 536) in *Chaetoceras decipiens* (fig. 213 I, J), where two sizes of these spores were observed. In the same year Bergon (13) recorded motile spores in a species of *Chaetoceras*, while Schiller (190) like Gran described two types of microspores in *C. Lorenzianum* (fig. 213 K, L).

A more detailed account was published by Bergon in 1907 of the formation of microspores in *Biddulphia mobiliensis* (14), a species in which he had already recorded them in 1902 (12). He described the formation within the frustules, after division of the protoplast (fig. 213 A), of two sporangia separated from one another by arched, non-silicified membranes (fig. 213 B) and giving rise usually to 32 rounded protoplasmic masses (fig. 213 C, *s*) which were liberated as swarmers with two laterally attached elongate flagella (fig. 213 D, E). Previously Karsten (97, 98) had reported microspores in *Corethron* (fig. 213 F) and, on rather slender evidence, suggested that they were motionless gametes. In 1914 Pavillard ((169) p. 167) reported the liberation of naked pear-shaped swarmers with two equal anterior flagella (fig. 213 H) in a marine *Coscinodiscus*, some of the swarmers possessing chromatophores being larger than the others which were colourless. More recently Henckel (72) records a formation of amoebae, escaping through a rupture in the envelope, in the cells of species of *Chaetoceras* and *Thalassiosira*, although the data leave it very open whether the phenomena are not due to the presence of parasites. The diversity exhibited by these various observations is striking.

The modern epoch commences with the work of Schmidt on *Melosira varians* (191), the first freshwater form in which microspores have been recorded. Schmidt describes successive formation of the latter to the number of eight in a cell (fig. 214 C). After the first

B, *Nitzschia fonticola* Grun., formation of first valve (*v*) on auxospore. C–E, *Gomphonema olivaceum* (Lyngb.) Kütz.; C, auxospore; D, the same prior to division; E, division. F, G, *Achnanthes subsessilis* Kütz.; F, division of protoplast; G, zygote (?) with fusing (?) nuclei. H–J, *Amphora Normani* Rabenh., possible autogamy; H, division of chromatophore; I, auxospore with two and J, with one nucleus. K–M, *Cocconeis placentula* Ehrenb. var. *lineata* Cl.; K, approximated individuals, nucleus on left in synapsis, on right in prophase; L, two young auxospores; M; nucleus in diakinesis. N, *Navicula amphisbaena* Bory and O, *Pinnularia viridis* Kütz., auxospores. *a*, auxospore; *m*, mucilage; *n*, nucleus; *p*, chromatophore; *v*, valve. (F, G after Karsten; N, O after West; the rest after Geitler.)

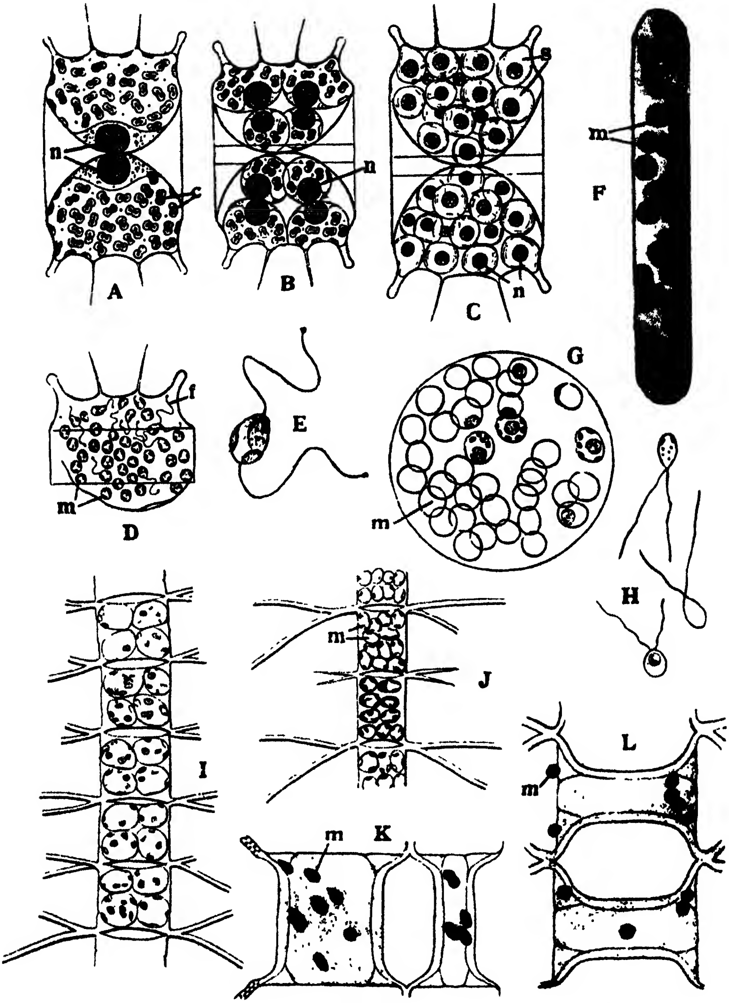

Fig. 213. Microspore-formation in Centrales. A–E, *Biddulphia mobiliensis* Bail. (after Bergon); A, development of the two sporangia; B, division into four; C, 16-celled stage; D, development of flagella; E, swarmer. F, *Corethron Valdiviae* Karst. (after Karsten), with microspores. G, H, *Coscinodiscus* sp. (after Pavillard); G, microspore-formation; H, swarmers. I, J, *Chaetoceras decipiens* Cl., two stages of microspore-formation (after Gran). K, L, *C. Lorenzianum* Grun. (after Schiller), two types of microspores. *c*, chromatophore; *f*, flagellum; *m*, microspore; *n*, nucleus.

division a pair of flagella is recognisable on each of the products. In some cases extrusion of chromatophores from the developing microspores was observed (fig. 214 C), so that the latter became colourless (cf. Pavillard). Naked bodies provided with chromatophores and four flagella were found outside the cells and were interpreted as zygotes (fig. 214 A, B). As Geitler(56) points out, Schmidt's figures give the impression that the phenomena noted by him might be due to the presence of a parasite, possibly one of the Chytridineae, and the same may apply to Pavillard's observations. The only point that speaks in favour of Schmidt's interpretation is that he observed the formation of new valves and connecting-bands within his quadriflagellate zygotes (fig. 214 B); such cases may, however, be due to the engulfment of an entire small individual.

Later the same author(192, 194, 195) investigated the microspores of *Biddulphia sinensis*, a common plankton form in northern seas, forming sporangia in the way described by Bergon. The accompanying cytological data have been largely withdrawn in his most recent paper(196*a*) after being strongly criticised by others versed in the interpretation of the cytology of Diatoms(56). Schmidt believes that there is a reduction of chromosomes during microspore-formation, but neither in *Biddulphia*, nor in *Melosira*, have any of the essential features of a reduction division been described.

There is some evidence for the occurrence of reduction during microspore-formation (cf. fig. 214 K, L) in *Coscinodiscus*. In *C. biconicus*, which forms 128 microspores by successive division, Hofker(73) counted twice as many chromosomes during the first five divisions as in the last two, although no distinctive phases of a reduction-division were observed. It would thus seem possible that meiosis takes place during the last two divisions in the cells forming microspores, although Schmidt(196) places it at a much earlier stage. On the whole it cannot be said that any really satisfactory proof of a reduction during microspore-formation has yet been provided.

The diverse data above taken under review (cf. also (105) p. 68) afford little evidence that the microspores are of the nature of gametes, since fusion has so far only been inferred and not actually established. Moreover, it is probable that in various cases a confusion with parasitic organisms has occurred. This statement must not, however, be taken as a denial of the existence of microspores which are clearly established as a method of multiplication in the Centrales. What remains doubtful is their fate. If the occurrence of reduction during their formation were clearly substantiated, the sexual nature of the microspores would be rendered very probable, but their exact rôle can only be proved by direct observation of living material. Both Murray(155 and Karsten ((101) p. 174) have recorded microspores of

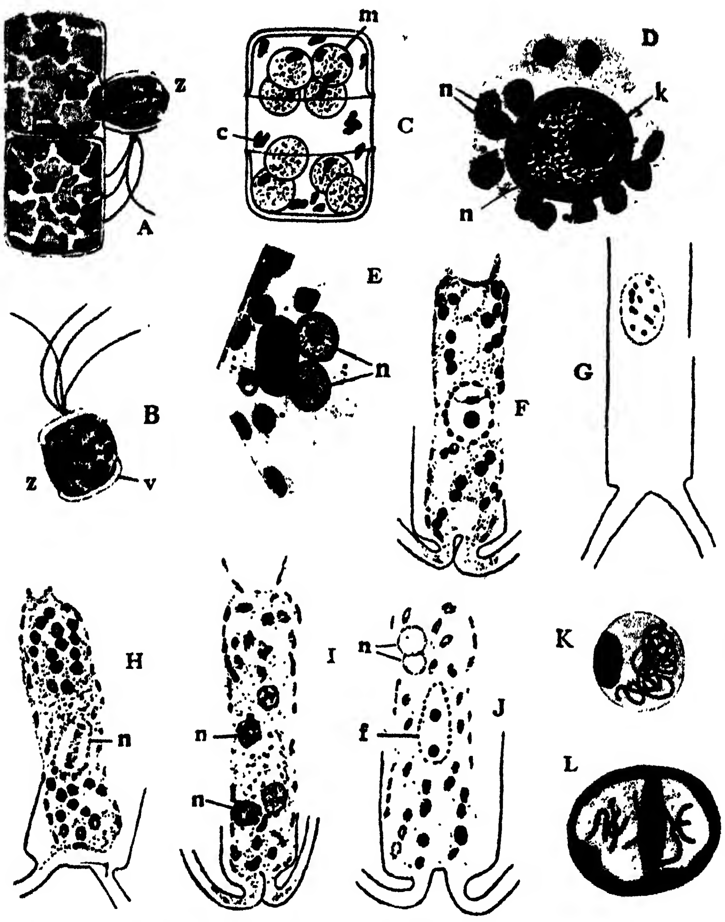

Fig. 214. Microspore-formation in Centrales. A–C, *Melosira varians* Ag.; A, B, two cells of a thread and "zygotes" forming new valves (cf. text); C, formation of microspores with extrusion of chromatophores. D, E, *Melosira arenaria* Moore, nuclei in young auxospore, D a later stage than E. F–J, *Chaetoceras borealis* Bail., successive stages in auxospore-formation (?); F, synapsis (?); G, diakinesis; H, first nuclear division; I, stage with four nuclei; J, supposed fusion-nucleus (*f*) and two degenerating nuclei (*n*). K, L, *Coscinodiscus apiculatus* Ehrenb., meiosis; K, synapsis; L, diakinesis (?). *c*, chromatophore; *k*, caryosome; *m*, microspore; *n*, nucleus; *v*, valve; *z*, zygote. (D, E after Cholnoky; F–I after Persidsky from Geitler; the rest after Schmidt.)

Coscinodiscus, in part already provided with new valves, in part still dividing, as occurring in large numbers in structureless mucilage (cf. also (215)) and a similar case is described by Bergon ((12) p. 135) for *Cyclotella*. This may imply a direct development of microspores, although Karsten regards such cases as examples of apogamy.

Geitler ((57) p. 11) has drawn attention to certain observations recorded by Went (229) and overlooked by later workers. Went describes how on a certain day the Atlantic plankton included as the only Diatoms two forms of *Chaetoceras*, of which the larger was invariably found to be forming microspores, while the smaller form showed no trace of division. These smaller individuals were, however, surrounded by swarms of flagellated cells corresponding in size to the microspores produced in the larger ones. Went suggests that these swarmers were microspores and that the undivided individuals of *Chaetoceras* surrounded by them were females about to be fertilised by the former. While this observation is also open to other interpretations (cf. (33 *b*) p. 716), Went's suggestion may prove to be correct and may explain why so far no one has ever seen fusion among the microspores. At the same time it should be recalled that Gran (66) and Schiller (190) found two types of microspores in *Chaetoceras*.

Against the inadequate evidence for the occurrence of reduction during microspore-formation we must place the data referred to on p. 620 which seem to imply a reduction during auxospore-formation. Persidsky (176), investigating auxospore-formation in two species of *Chaetoceras*, found that it took place with a probable reduction-division, both synapsis and diakinesis stages (fig. 214 F, G) being recorded, although the former is perhaps rather questionable. Persidsky believed that two of the four resulting nuclei (fig. 214 I) subsequently aborted, whilst the other two fused (fig. 214 J). Cholnoky (33 *b*) has recently produced data indicating a similar state of affairs in *Melosira arenaria* (fig. 214 D, E). The mere fact of division of the nucleus into four suggests a reduction-division. Both these investigators regard the microspores as asexual reproductive cells. Geitler ((57) p. 12) points out that in one of Persidsky's figures three of the nuclei are smaller than the fourth (cf. fig. 214 I) and that the evidence for nuclear fusion is not convincing. He suggests that possibly Persidsky's stages may mark the reduction-division in a female cell to be fertilised after the manner suggested by Went's observations. Microspore- and auxospore-formation are not, however, found to synchronise as far as present data go, but to occur in different phases of the life-history.

Whatever may ultimately prove to be the correct reading of all these facts, it now seems clear that the Centrales are diploid like the Pennales, and the view that the former were haploid, which held sway for some little time on a rather inadequate basis, may be regarded as of historical interest only.[1] On any interpretation the sexual

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[1] Karsten (97) assumed that in *Corethron* reduction took place in the germination of the supposed zygotes, but in a recent paper ((103) p. 10) he appears

reproductive process would appear to be specialised as compared with that of the majority of the Pennales.

Subdivision of the protoplast to form a number of rounded masses has been recorded among Pennales in *Eunotia lunaris* (75) and in *Surirella spiralis* (232); in the latter case the structures in question were provided with thick walls (fig. 215 A). Recently Kolbe ((108) p. 99) has met with similar stages in *Nitzschia vitrea* and concludes that they are due to a division and agglomeration of the chromatophores into rounded balls in which the apparent nuclei are pyrenoids. This explanation can, however, hardly apply to the case of *Surirella* where the structures in question make altogether the impression of being reproductive bodies (fig. 215 A). However that may be, it seems clear that they are not of the same nature as the microspores of Centrales.

THE RESTING STAGES OF DIATOMS

Auxospores are not resting stages, but a means of rejuvenescence. Very little is known as to the manner in which Diatoms persist from one period of activity to another. In the case of pennate forms we must assume that this is usually accomplished by surviving vegetative individuals, although resting spores have been recorded in *Fragilaria* and *Achnanthes taeniata* ((101) p. 195). Many Diatoms are known to be capable of withstanding considerable drought (cf. (8), (87) p. 171) and they are also resistant to cold (130). According to Petit (178) they can withstand gradual drought, the protoplast then withdrawing to one end of the cell. Even after several months in this condition complete recovery is possible.

In Centric Diatoms, especially among the pelagic forms, definite resting spores have frequently been observed. In *Attheya Zachariasi* (201, 205) and in *Chaetoceras* (64, 66, 67, 98, 207) the protoplast contracts to the centre and secretes successively two thick-walled valves, no girdle being formed (fig. 215 B, *a–d*). In *Chaetoceras* the valves lack the characteristic horns of the vegetative cells, though often provided with elaborate processes (fig. 215 C). These are present, however, only on the epitheca; the later-formed hypotheca is smooth. The spores of *Melosira* (64, 154) are formed in pairs after a cell-division (fig. 215 E). In the species of *Rhizosolenia* (159, 201, 205, 208) one or two thick-walled spores arise after a strong contraction of the protoplast (fig. 215 D, *s*). According to Schulz (205) spore-formation in *Attheya* and *Rhizosolenia* is preceded by a nuclear division and an increase in

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to have abandoned this doubtfully founded view, since he speaks of the Diatoms as being uniformly diploid. It is presumably on this view of Karsten's that Hustedt's statement ((87) p. 9) is based that the Centrales are haploid and that reduction occurs in the zygote, for which there is at present no reliable evidence whatever.

the number of intercalary bands in one theca. The germination of these spores has so far not been observed.

In certain Centrales of the oceanic plankton a marked dimorphism of the individuals has been established (see (87) p. 129), the one form being much coarser than the other and clearly less well adapted to a planktonic existence. Thus, in *Rhizosolenia hebetata* (66) the winter-(resting?) form has broader frustules with much thicker walls than the normal ones; moreover, the former lacks the long spines found on the valves of the latter. A similar dimorphism has been observed in *Eucampia balaustium* (98), where the thick-walled form inhabits much deeper layers of the sea than the thin-walled one. It is probable that in all such cases the coarser form represents the means of perennation from one period of planktonic activity to the other (66). A similar condition is known for the freshwater *Melosiras* (34).[1]

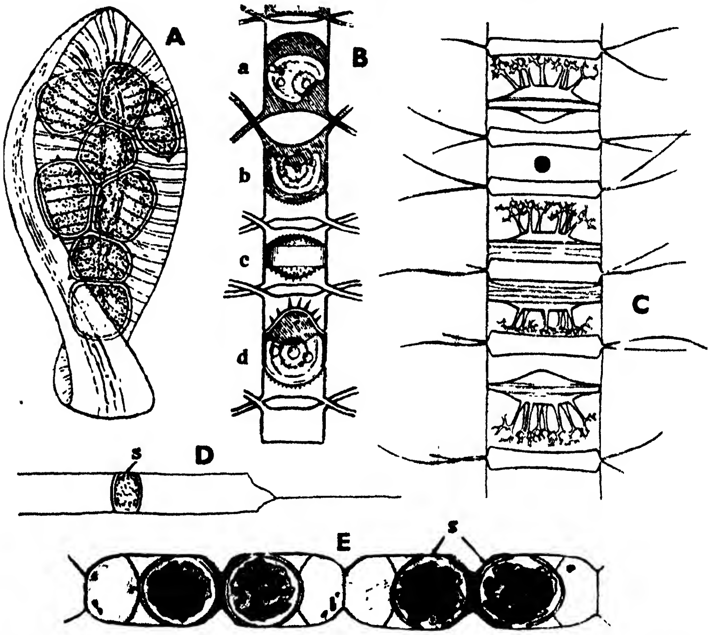

Fig. 215. A, *Surirella spiralis* Kütz., spore-formation. B, *Chaetoceras paradoxum Schüttii* Cl., stages in spore-development; *a*, *b*, formation of first valve; *c*, *d*, fully developed spores, *c* from the surface, *d* in optical section. C, *Chaetoceras* sp., at either end mature spores, the two middle ones with only one valve formed. D, *Rhizosolenia morsa* West, resting spore (*s*). E, *Melosira hyperborea* Grun., paired resting-spores (*s*). (A, D after West; B after Schütt; C after Pascher; E after Gran.)

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[1] For other examples of such dimorphism, see (153), (203), (226), (230).

CLASSIFICATION AND INTERRELATIONSHIPS OF DIATOMS

The classification adopted by Hustedt (87) and Karsten (101), which appears to correspond best with our present knowledge of the class, is as follows (nomenclature based on Hustedt):

A. *Centrales:* Valves with centric structure, markings not arranged along two lines; no raphe or pseudoraphe; no movement. Chromatophores commonly numerous. Auxospores apparently formed without conjugation.

(*a*) *Discoideae:* Cells shortly cylindrical or disc-shaped; valves circular, hyaline, areolated or with radiating striations, usually without special processes (*Arachnoidiscus*, *Coscinodiscus*, *Cyclotella*, *Melosira*, *Planktoniella*, *Sceletonema*, *Stephanodiscus*, *Stephanopyxis*, *Thalassiosira*).

(*b*) *Solenoideae:* Cells elongate, cylindrical or subcylindrical, circular or broadly elliptical in cross-section; girdle complex, with numerous intercalary bands (*Corethron*, *Dactyliosolen*, *Rhizosolenia*).

(*c*) *Biddulphioideae:* Cells box-shaped, valves with two or more poles, mostly provided with horns or bosses (*Attheya*, *Bacteriastrum*, *Biddulphia*, *Chaetoceras*, *Hemiaulus*, *Isthmia*, *Terpsinoë*, *Triceratium*).

(*d*) *Rutilarioideae:* Valves naviculoid; markings radially arranged or irregular (*Rutilaria*).

B. *Pennales:* Valves isobilateral, medianly zygomorphic, or less frequently dorsiventral, never centric; valve-view mostly boat- or needle-shaped, with markings arranged pinnately in relation to a raphe or pseudoraphe; movement in many forms; chromatophores commonly large and few; auxospores (except in Araphideae) normally formed by conjugation.

I. *Araphideae:* Only a pseudoraphe present.

(*e*) *Fragilarioideae:*[1] Valves mostly straight, rod-shaped or lanceolate (*Asterionella*, *Ceratoneis*, *Climacosphenia*, *Diatoma*, *Fragilaria*, *Grammatophora*, *Licmophora*, *Meridion*, *Rhabdonema*, *Striatella*. *Synedra*, *Tabellaria*).

II. *Raphidioideae:* Showing the beginnings of a raphe, extending for a short distance from the polar nodules; no central nodules.

(*f*) *Eunotioideae:* Raphe on one (Peroniaceae) or on both (Eunotiaceae) valves (*Eunotia*, *Peronia*).

III. *Monoraphideae:* Fully developed raphe only on one valve.

(*g*) *Achnanthoideae:* Frustules crooked or suddenly bent in the girdle-view; one valve with a pseudoraphe only (*Achnanthes*, *Cocconeis*, *Rhoicosphenia*[2]).

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[1] This group is probably artificial, since some of the forms may be primitively devoid of a raphe, whilst others (e.g. *Synedra*) may have lost it secondarily.

[2] Karsten refers *Rhoicosphenia* to the Naviculoideae.

IV. *Biraphideae:* Both valves with a fully differentiated raphe.

(*h*) *Naviculoideae:* Raphe occupying the apical axis, usually without a keel, but when a keel is present, without carinal dots (*Amphipleura, Amphiprora, Amphora, Cymbella, Frustulia, Gomphonema, Gyrosigma, Mastogloia, Navicula, Pinnularia, Pleurosigma, Stauroneis*).

(*i*) *Epithemioideae:* Raphe not occupying the apical axis, sometimes on an excentric keel, without carinal dots (*Denticula, Epithemia, Rhopalodia*).

(*j*) *Nitzschioideae:* Both valves with a canal-raphe, situated in a keel lying on the valve-face and often excentric, with carinal dots (*Bacillaria, Cylindrotheca, Hantzschia, Nitzschia*).

(*k*) *Surirelloideae:* Valves with two lateral wings occupied by the canal-raphe, the latter connected by canals with the protoplast (*Campylodiscus, Cymatopleura, Surirella*).

The two main orders of Diatoms clearly show marked differences and these have at times led to a suggestion that the resemblances may be due to homoplasy and that the two series may have had a distinct origin ((43), (158) p. 194, (175)). Whilst such a possibility cannot be gainsaid, there is little that at the present time speaks positively in its favour. The strongest argument is perhaps to be found in the apparent diversity in reproductive methods. Even if, however, the microspores of Centrales should ultimately prove to be gametes, a divergence of the two series from a common ancestry, in view of the many points of contact (general structure, similar pigmentation, apparently similar metabolism, the diploid character), would still remain probable. Karsten ((101) p. 182) has put forward the view that the production of auxospores by sexual fusion in the majority of the Pennales has resulted from the acquisition of motility by the latter, since in the Tabellariaceae, which are devoid of a raphe, auxospore-formation appears to take place in a manner very similar to that found in Centrales (cf. p. 620). This is plausible and, in the event of the microspores of Centrales proving to be gametes, it would mean that the sexual process has evolved in different directions in them and in the Pennales. Karsten believes that the Tabellariaceae are allied to some of the Centrales by way of such forms as *Terpsinoë* which possesses naviculoid valves provided with numerous transverse septa (fig. 191 L, p. 576).

It may not, however, be amiss to point out that there is scarcely enough evidence at present to establish definitely the view that the Araphideae are primitive, since some and perhaps all may equally well be reduced forms. Similarly, the Raphidioideae (Eunotioideae) may be forms with a reduced raphe and not one in course of differentiation. In other words it may be that we shall have to read the sequence in the opposite direction and to regard the Centrales as the most highly evolved group which in correspondence with its adaptation to a mainly planktonic existence has given up the equipment that allowed of motility in the essentially bottom-living Pennales. Peragallo (175) regarded the *Nitzschias* as nearest the ancestral type. Should the phenomena described by Went and detailed on p. 637 prove to be of the nature of sexual reproduction, the Centrales would be more highly evolved than the Pennales also in this respect.

It is, however, significant that the oldest known fossil Diatom deposits contain a large number of centric forms (*Melosira*, *Cyclotella*, *Stephanodiscus*, *Coscinodiscus*, *Stephanopyxis*, cf. (70), (181) pp. 44, 693). Hanna (68) found only Centric Diatoms in a Cretaceous deposit from California. Pia ((181) p. 52) concludes that at the period of the maximum development of Diatoms in the Miocene centric forms preponderate (cf. also (40), (41)). Most of the extinct genera belong to Centrales and many genera represented by numerous species in the past have now only a few living ones. These data seem to support the view that the Centrales are older than the Pennales, although it is possible that the preponderance of the former is a consequence of the fossil deposits being marine. There is no satisfactory evidence of the occurrence of Diatoms in the Palaeozoic (41 *a*, 180, 182).

Since the siliceous envelopes of Diatoms are practically imperishable large deposits (oceanic and lacustrine) are laid down wherever Diatom life is abundant. Not only are such deposits being formed at the present day (especially in the Arctic and Antarctic Oceans), but similar diatomaceous earths (Kieselguhr), often of immense thickness, are evidence of the abundant Diatom life in former eras (cf. (39)). These diatomaceous deposits are associated principally with rocks of Tertiary age and are found at Dolgelly in Wales and Toome Bridge in Antrim, Ireland, but much more extensive ones occur in other parts of Europe and especially in America ((180 *a*) p. 92, (221) p. 192).

RELATIONSHIPS OF DIATOMS WITH OTHER CLASSES

As already pointed out, the suggested relationship of Diatoms with Desmids is based merely on superficial resemblances. Pascher (164) has strongly supported a relationship between Bacillariophyceae, Xanthophyceae, and Chrysophyceae and advocates a union of these three classes in a division Chrysophyta, as opposed to the true green forms, the Chlorophyta. According to his view the Diatoms occupy much the same position in the Chrysophyta as the Conjugales do among the Chlorophyta, but it must be recognised that Diatoms offer a considerably sharper contrast to the other Chrysophyta than do the Conjugales to the remaining Chlorophyta.

Pascher's view is based on a number of similarities, viz. preponderance in all three classes of carotinoid yellow or brown pigments in the chromatophores, the associated absence of starch and occurrence of oil as one of the usual assimilatory products, and certain resemblances in the structure of the cellular envelopes. These may well indicate a physiological relationship of some significance. Deposition of silica in the membrane is a feature of all three classes (mainly in the cysts in Xanthophyceae and Chrysophyceae), and the bivalved structure of the cell-wall typical of the ordinary diatom-frustule is seen both in the vegetative cells and the resting-stages of various Xanthophyceae, while the cysts of Chrysophyceae likewise always have an envelope composed of two pieces (cf. p. 509). The resting-spores (endogenous cysts) formed by *Chaetoceras* (fig. 215 B, C) much resemble those of Chrysophyceae ((164) p. 244, (165)). In *Ophiocytium*, *Tribonema*, and probably in other members of the Xanthophyceae the cell-walls consist of numerous thimble-like segments (cf. p. 488); the same structure is repeated in the envelopes of *Dinobryon*, *Hyalobryon*, and other Chrysophyceae (p. 530), and is paralleled in those Diatoms in which intercalary bands are interposed in considerable numbers between the valves and their connecting-bands (cf. e.g. *Rhabdonema*, fig. 190 A, p. 574). The presence of leucosin in certain Diatoms (110) is also of note from this point of view.

Recently Pascher has shown that in certain Xanthophyceae (e.g. *Chloromeson*, p. 473 and fig. 154 O) the cysts are formed endogenously in exactly the same manner as in Chrysophyceae. In fact *Chloromeson*, except for its yellow-green colour, shows scarcely any essential differences from an *Ochromonas*, and its discovery lends very great support to a close affinity between Xanthophyceae and Chrysophyceae. The derivation of these two classes from a common motile ancestry is now more than probable. As regards Diatoms, we have to do with a highly specialised class and, whilst the points of similarity to the other two emphasised by Pascher are significant, the absence of any clear connecting forms renders a full evaluation of the evidence difficult.

Schütt (210) and others (175) have assumed an affinity between the Bacillariophyceae and Dinophyceae, based mainly on a certain similarity in pigmentation and the products of assimilation, but the fundamental organisation of the latter class is so essentially different that there is no basis for such a view.

Literature of Bacillariophyceae

1. ALLEN, E. J. 'On the culture of the plankton diatom *Thalassiosira gravida* Cleve in artificial sea-water.' *Journ. Marine Biol. Assoc. Plymouth*, **10**, 417–39, 1914. **1a.** ALLEN, E. J. & NELSON, E. W. 'On the artificial culture of marine plankton organisms.' *Ibid.* **8**, 421–74, 1910. **2.** BACHMANN, H. '*Cyclotella bodanica* var. *lemanica* O. Muller im Vierwaldstättersee und ihre Auxosporenbildung.' *Jahrb. wiss. Bot.* **39**, 106–33, 1903. **3.** BACHRACH, E. & DHÉRÉ, C. 'Sur la fluorescence d'une Diatomée marine et

Class V. CRYPTOPHYCEAE

This class, which appears to be equally scantily represented in the sea ((38), (39) p. 86) and in freshwaters, is as yet but very imperfectly known. Enough has come to light, however, to bring out clearly some of the essential characteristics and to show that much the same evolutionary sequence has been followed as in the other great flagellate-algal series. The class includes the rather specialised flagellate Cryptomonadales and a small number of algal types. Unless, however, many of the latter are still to be discovered or have become extinct, it would appear that the Cryptophyceae have passed but little beyond the confines of flagellate organisation. No filamentous forms are known.

Order I. *CRYPTOMONADALES*

The Family Cryptomonadaceae

The naked motile type is developed in its most typical form in the Cryptomonadaceae.[1] The individuals exhibit a pronounced dorsiventral construction, the cells being prominently flattened in the dorsoventral plane, so that the cross-section is oval or elliptical (fig. 216 C, J). When the individuals lie on one of their broader faces (side-view), the anterior extremity appears obliquely truncate or emarginate and is not uncommonly prominently protruded at the dorsal corner (fig. 216 H); the dorsal margin is convex, the ventral margin usually flat or concave (fig. 216 A, B, K). Passing over the anterior extremity, where it produces a more or less marked constriction, is a longitudinal furrow which extends as a curved line obliquely over the flanks to die out sooner or later without reaching the posterior end (fig. 216 A, B, K, L, *f*).

In most genera (*Cryptomonas*, fig. 216 B; *Rhodomonas* (20), fig. 216 H) there is a tubular gullet (*g*) extending from the anterior end of the furrow more or less deeply into the interior of the protoplast, but in others (*Cryptochrysis*, fig. 216 I, K, L) this is stated to be lacking. Two somewhat unequal flagella arise at the anterior end, either from the furrow or from the ventral edge of the aperture of the gullet (fig. 216 A, H, L). The flagella are slightly band-shaped with a thread-like termination and arise from closely approximated basal granules (fig. 217 D, *b*); these, in *Chilomonas*, are connected to delicate, closely contiguous rhizoplasts (*r*) which extend either to the nucleus or to

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[1] See (8–10), (25), (29), (34), (41).

the posterior end of the individual (1, 2, 34a); a similar condition seems to obtain in *Cyathomonas* (fig. 217 N).

In *Rhodomonas*, according to Zimmermann (47), the rhizoplast is connected with the pyrenoid. According to Dellinger (11a) the flagella of *Chilomonas* consist of four fibrils spirally wound round one another, but such a structure has been recorded by no other worker. In *Cryptochrysis*, Pascher (27) states that the one flagellum shows the usual lashing movements, whilst the other performs undulatory movements (cf. also (45) p. 290). Many species of *Cryptomonas* exhibit a characteristic swaying of the individuals, first to one side and then to the other, during movement (13, 23), although others exhibit the usual rotation.

The nuclei ((2), (2a) p. 60, (35)) have a prominent caryosome and finely dispersed chromatin in the outer nucleus (fig. 216 O); the caryosome is stated to include one or two centrosomes (1, 2). Division of the nucleus sometimes takes place amitotically. The chromosomes are small and granular (fig. 216 Q).

The nucleus is usually situated near the posterior extremity (fig. 216 B, K, *n*) and is in contact with the pyrenoid in *Rhodomonas*. The periplast is firm but elastic, sometimes with longitudinal striations (fig. 217 N). The cells are not ordinarily metabolic, although Zimmermann (47) records changes of form on the part of *Rhodomonas baltica* when pushing its way between foreign bodies.

There are usually two large and often lobed parietal chromatophores, mostly apposed to the dorsal and ventral margins[1] respectively (fig. 216 B, E, F), though in *Rhodomonas* (fig. 216 G) there is only one. In *Cryptochrysis polychrysis* (29) (fig. 216 I) and *Cyanomonas* (12)[2] (fig. 216 M) the chromatophores are numerous and discoid. Their pigmentation is variable, even in the same mass of material, but diverse shades of brown are probably the most frequent; apart from these, red (*Rhodomonas*), olive-green, and blue-green (*Chroomonas* (17); *Cyanomonas*; *Cryptomonas coerulea* Geitler (15)) tints occur. Deep-water forms are not uncommonly red (15, 32). Nothing is known about the nature of the pigments, but Pascher ((29) p. 96) affirms their similarity to those of the Dinophyceae. Rounded pyrenoid-like bodies, which are apparently not embedded in the chromatophores (fig. 216 A, D, E, G, *p*), are usually present, though sometimes lacking in *Cryptomonas*. Usually there is a single pyrenoid in the middle of the cell, but there may be several ((11), (16) p. 361). In *Rhodomonas* (47) they have been shown to be embedded in an enlargement of the chromatophore (fig. 216 J), and possibly this will also prove to be the case in the other genera.

After active photosynthesis the products are stored as solid discoid

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[1] In *Cryptomonas anomala* (13) they are apposed to the flanks (fig. 216 D).

[2] First described as *Cryptoglena americana* and renamed *Cyanomonas* by Oltmanns (25).

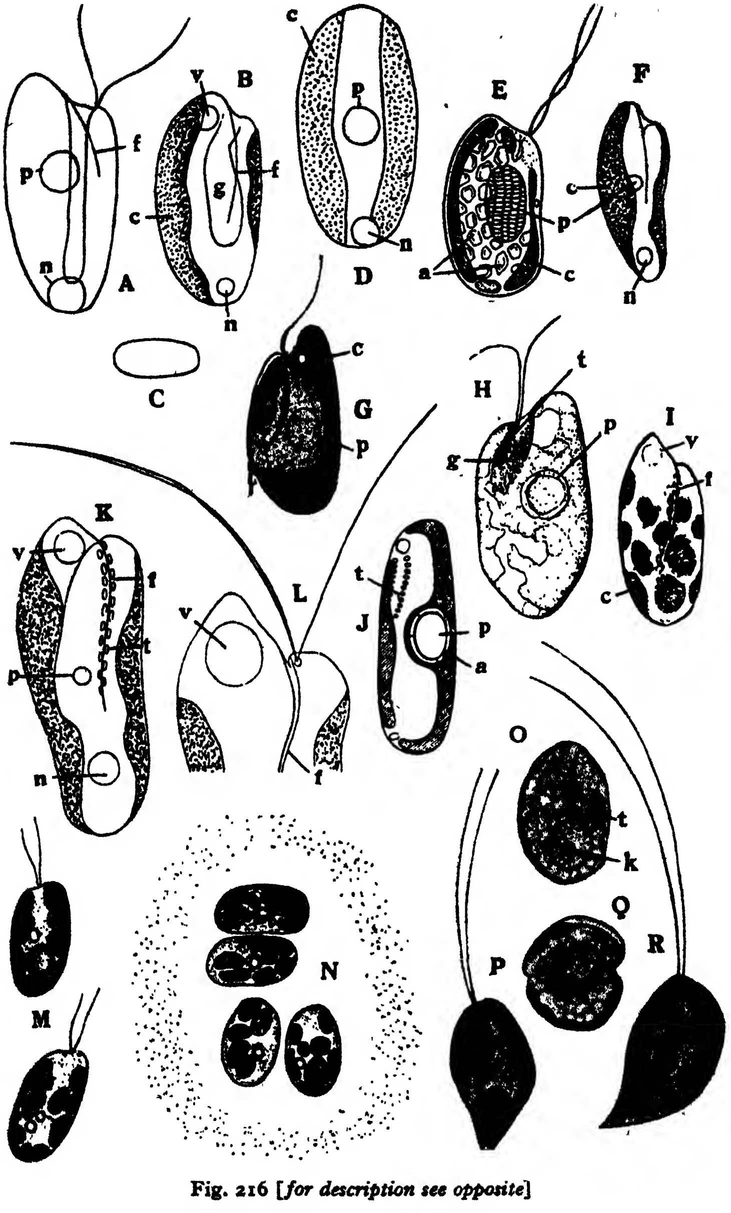

Fig. 216 [*for description see opposite*]

granules ((7) p. 215), which in *Cryptomonas* give a blue coloration with iodine and appear to be a form of starch, whilst in other cases (e.g. *Cryptochrysis*) iodine colours them reddish or reddish violet. These granules form a shell round the pyrenoids (fig. 216 E, H, J, *a*), as well as covering the inner surface of the chromatophores (fig. 216 E, *a*). Both in reaction and mode of deposition there is a distinct resemblance with Floridean starch ((16) p. 360).

A prominent contractile vacuole which discharges into the furrow, or into the gullet when present, is situated anteriorly, usually on the dorsal side (figs. 216 B, K; 217 D, *v*); in *Cyathomonas*, however, it is located ventrally (fig. 217 N, *v*). In some species there is more than one of these vacuoles. The furrow or gullet is often lined with small rod-shaped colourless and highly refractive trichocysts (figs. 216 H, K; 217 D, *t*). When the individuals are subjected to injurious influences, long threads are suddenly protruded from these trichocysts into the gullet. The latter appears to have nothing to do with ingestion, all Cryptomonadales, except *Cyathomonas* (cf. p. 657), being holophytic or saprophytic.

Hillea ((39) p. 87), an incompletely known form recorded from the Adriatic, possibly represents a relatively primitive type of the Cryptomonadaceae to which all the genera previously discussed belong. It lacks the marked furrow of other forms, its place being taken by a shallow depression confined to one surface (fig. 216 P, R). The cells, which run to a point at the posterior end, show a limited amount of metaboly and are stated to possess two equal flagella. A better knowledge of this form will perhaps help to elucidate the origin of the elaborate organisation found in the bulk of the members of the Cryptomonadaceae.[1]

[1] Another isolated form is the uniflagellate *Monomastix* (fig. 217 I–K) described by Scherffel (37). The somewhat metabolic individuals have two lateral greenish chromatophores, each with a pyrenoid (*p*); there is a stigma (*s* not far from the posterior end where a number of rod-shaped trichocysts (*t*) are situated. The anterior extremity bearing the flagellum is sometimes obliquely truncate (fig. 217 J). This form, together with *Phacomonas* (p. 473), *Mesostigma* ((22*a*) p. 395), and others is placed by Korschikoff (22) in a group Protochlorinae which he regards as allied to the Volvocales. The evidence of affinity is, however, hardly satisfactory.

Fig. 216. Cryptomonadaceae. A, D, *Cryptomonas anomala* Fritsch; A from the side, D from the dorsal surface. B, E, O, Q, *C. ovata* Stein; B, E, side-views; O, nucleus in prophase; Q, anaphase. C, *C. compressa* Pascher, optical section. F, *Chroomonas Nordstedtii* Hansg. G, H, J, *Rhodomonas baltica* Karst.; J, view from the edge. I, *Cryptochrysis polychrysis* Pascher. K, L, *C. commutata* Pascher; L, enlarged anterior end. M, N, *Cyanomonas americana* (Davis) Oltm.; N, palmelloid stage. P, R, *Hillea fusiformis* Schill. *a*, starch; *c*, chromatophore; *f*, furrow; *g*, gullet; *k*, caryosome; *n*, nucleus; *p*, pyrenoid; *t*, trichocysts; *v*, vacuole. (A, D after Fritsch; E after Senn; G after Karsten; H, J after Zimmermann; M, N after Davis; O, Q after Belar; P, R after Schiller; the rest after Pascher.)

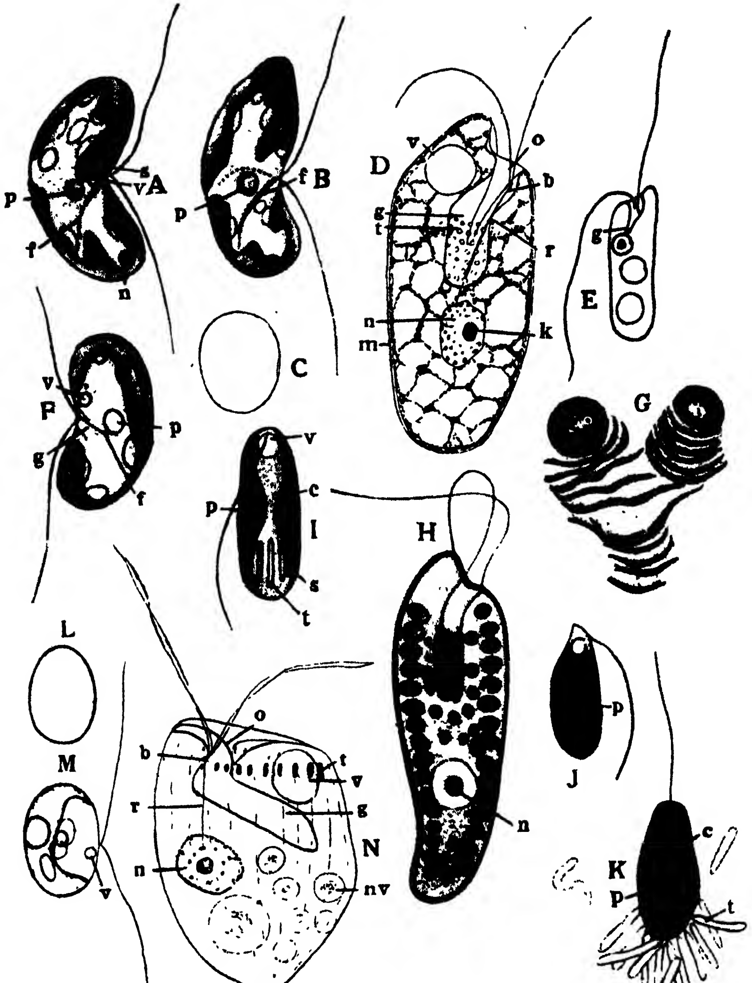

Fig. 217. A–C, *Protochrysis phaeophycearum* Pascher; A, B, from the side; C, optical transverse section. D, H, *Chilomonas Paramaecium* Ehrenb. E, *Phyllomitus amylophagus* Klebs. F, *Nephroselmis olivacea* Stein. G, *Cryptomonas ovata* Stein, germinating cysts with stratified mucilage-stalks. I–K, *Monomastix opisthostigma* Scherff.; K, individual with excreted trichocysts (*t*). L, M, *Sennia commutata* Pascher; L, optical transverse section. N, *Cyathomonas truncata* Ehrenb. *b*, basal granules; *c*, chromatophore; *f*, furrow; *g*, gullet; *k*, caryosome; *m*, periplast; *n*, nucleus; *nv*, nutritive vacuole; *o*, aperture of gullet; *p*, pyrenoid; *r*, rhizoplast; *s*, stigma; *t*, trichocysts; *v*, vacuole. (D, N after Ulehla; E after Lemmermann; G after Senn; H after Bütschli; I–K after Scherffel; the rest after Pascher.)

THE FAMILY NEPHROSELMIDACEAE

As in other series of motile unicellular forms, there are interesting special developments among the Cryptomonadales. Thus, in the Nephroselmidaceae (27, 28) (*Protochrysis*, fig. 217 A–C; *Nephroselmis*, fig. 217 F) the body is kidney- or bean-shaped and the two flagella are attached laterally, a little below the middle of the concave surface, the shorter being directed forwards, the longer trailing behind during movement. The furrow (*f*) runs more or less transversely. An eye-spot (*s*), which is as yet not recorded in any member of the true Cryptomonadaceae, is situated just below the point of origin of the flagella. In *Nephroselmis*[1] (fig. 217 F) there is a gullet (*g*), likewise commencing in the middle of the concave surface and curving towards the posterior end. A more doubtful form is the relatively simple *Sennia*[1] (fig. 217 L, M), in which according to Pascher occasional indications of a furrow are to be found. The small cells are practically oblong and devoid of the lateral emargination of other Nephroselmidaceae.

There is an undoubted resemblance between the Nephroselmidaceae and the swarmers of Phaeophyceae, first pointed out by Pascher ((26) p. 199), but the resemblance appears to extend only to morphological features and there is no clear evidence of any similarity in pigments or products of assimilation; nor is there in the Phaeophycean swarmer anything to correspond to the furrow or the gullet of these forms (cf. also (30) p. 153). The Nephroselmidaceae have so far mainly been found in fresh water, but Schiller (39) has described a species of *Nephroselmis* from the Adriatic.

COLOURLESS AND SYMBIOTIC TYPES

The colourless type is represented among Cryptomonadaceae by the saprophytic *Chilomonas* (10, 12 a, 24, 45) and the holozoic *Cyathomonas* (12 a, 18, 45). *Phyllomitus* (20 a) (fig. 217 E), usually classed among the Protomastigineae, probably also belongs here ((31) p. 39). *Chilomonas* (fig. 217 D, H) closely resembles a *Cryptomonas*, but lacks chromatophores and pyrenoids, though forming starch (cf. *Polytoma*). In *Cyathomonas* (fig. 217 N), in which the individuals have a somewhat

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[1] It may perhaps be open to doubt whether the form that Pascher calls *Nephroselmis olivacea* is identical with Stein's form, but it shares with it the reniform shape. The organism described by Senn (42) is, on the other hand, obviously quite different and is justifiably referred to a distinct genus *Sennia* by Pascher (28). Senn ((40) p. 187, (43)) believes that his form is one of the Volvocales, and Klebs ((21) p. 420) held the same view with reference to *Nephroselmis*, but the brown coloration of the chromatophore and the orientation of the flagella are altogether against this. There is some doubt about the nature of the cellular inclusions in these diverse forms.

different shape, the aperture of the gullet (*g*) is surrounded by a wide ring of denser cytoplasm containing a series of ovoid glistening bodies which are probably trichocysts (*t*). Bacteria, etc., are absorbed through the gullet in nutritive vacuoles (*nv*) which are to be found in all parts of the body, the undigested remnants being subsequently extruded through the gullet. Food is stored in the form of fat.

The yellow cells found in numerous animals, especially Radiolarians (fig. 218 A, B, *a*), and usually described under the name of *Zooxanthella* (3, 4, 4*a*, 14, 46) are symbiotic organisms which no doubt in large part belong to the Cryptomonadales.[1] Pascher (26) suggests the name of *Chrysidella* for those certainly established as belonging to this group. Only relatively few Radiolarians lack these cells, and in some species they occur in very large numbers, although in others only a few individuals are present. In most cases the yellow cells lie in the peripheral parts of the animal (fig. 218 A, B). As a general rule the larval stages of the latter appear to be devoid of the symbiont, so

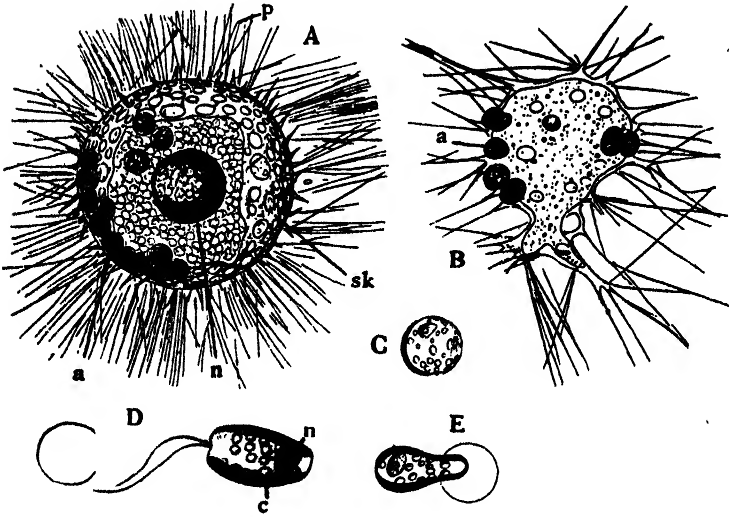

Fig. 218. *Zooxanthellae* in Radiolaria. A, *Acrosphaera spinosa* and B, *Collozoum inerme*, with the algal cells (*a*). C, single *Zooxanthella*. D, swarmer next to empty cell. E, escape of protoplast. *c*, chromatophore; *n*, nucleus; *p*, rhizopodia; *sk*, skeleton of animal. (All after Brandt.)

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[1] According to Hovasse and Teissier (19), however, the Zooxanthellae of diverse Coelenterata show cytological features that indicate a reference to Dinophyceae.

that a fresh infection of each generation is necessary. When motile reproductive stages are produced by the animal or when the latter dies, the Zooxanthellae are set free in the living condition and can then multiply to form small palmelloid masses. Both here and within the animal body the cells are enveloped by a thin cellulose wall (fig. 218 C), so that since this coccoid state evidently predominates these forms should perhaps be classed with the Cryptococcales (p. 661). The motile stages which are liberated from the motionless cells (fig. 218 D, E) appear to lack a gullet and therefore show the simpler organisation of a *Cryptochrysis*.

There can be little doubt that the association is in most cases, as in that of the *Zoochlorellae* (p. 186), of the nature of a symbiosis. Geddes (14) showed the evolution of oxygen from the yellow cells and it has been suggested that the factors controlling the depth at which reef-building corals can live may lie in the conditions being suitable for the photosynthesis of associated *Zooxanthellae* (44). On the other hand Boschma (3) believes that in the case of Coelenterata the relation is more one of parasitism of the animal on the alga.

REPRODUCTION OF THE CRYPTOMONADALES

Reproduction in the Cryptomonadales is effected in the usual way by longitudinal division, generally during the motile phase, although in most species of *Cryptomonas* for example the dividing cells come to rest and become embedded in mucilage, often forming extensive palmelloid groups; the same is seen in *Cyanomonas* (fig. 216 N). Sometimes in *Cryptomonas*, as a result of one-sided mucilage-production, rough dendroid groups of cells borne on short thick stratified mucilage-stalks are formed (fig. 217 G). According to Ulehla ((45) p. 287) both gullet and vacuole are halved during division, while in motile individuals one daughter receives the flagella of the parent, while the other forms them afresh. Thick-walled cysts, with a membrane containing cellulose, are known in various members of the order. In forms with a firm periplast (e.g. *Chilomonas*) they may develop endogenously.

PALMELLOID TYPES (PHAEOCAPSINEAE)

The only members of this suborder are *Phaeococcus* ((26) p. 463)[1] and *Phaeoplax* ((26) p. 197),[2] but the assignation of the former to the Cryptophyceae remains doubtful. *Phaeococcus Clementi* (fig. 219 A) is terrestrial, forming small gelatinous masses with a stratified mucilage-

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[1] As Pascher has shown, Borzi confused two Algae in his description of this form (cf. p. 554).

[2] This was described by Reinisch (36) under the name of *Phaeococcus marinus*.

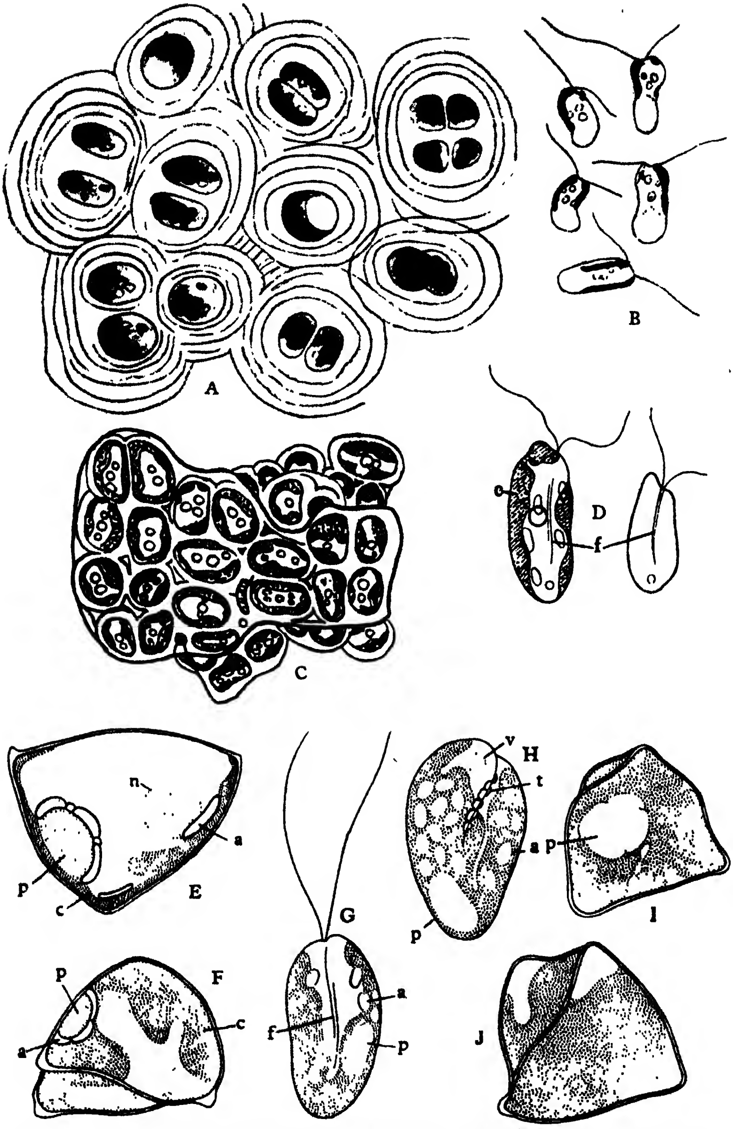

Fig. 219. A, B, *Phaeococcus Clementi* Borzi (after Borzi); A, part of a stratum; B, swarmers. C, D, *Phaeoplax marinus* (Reinisch) Pascher (after Reinisch); C, part of stratum; D, swarmers. E–J, *Tetragonidium verrucatum* Pascher (after original drawings kindly furnished by Prof. Pascher); E, F, I, J, coccoid cells in various aspects; G, H, swarmers. *a*, starch; *c*, chromatophore, *f*, furrow; *n*, nucleus; *p*, pyrenoid; *t*, trichocyst; *v*, vacuole.

envelope. *Multiplication* is effected by swarmers with two lateral chromatophores and two unequal flagella (fig. 219 B). Cotton (6) and Carter (5) record a species, *P. adnatus* (Naeg.) West, from habitats in the neighbourhood of the sea, but this, even more than Borzi's species, gives the impression of being one of the Chrysocapsineae (p. 541).

Phaeoplax (fig. 219 C), so far only observed in marine cultures, forms similar gelatinous lumps in which the envelopes of the cells give cellulose-reactions. The swarmers (fig. 219 D), which appear to escape singly from the cells of these palmelloid stages, very closely resemble a *Cryptochrysis*, having the same dorsiventral form with a furrow lined with glistening granules, apically attached flagella, and a pyrenoid enveloped by a sheath of solid granules which stain reddish violet with chlor-zinc-iodide.

Order II. *CRYPTOCOCCALES*

Pascher ((30) p. 160) in 1914 briefly described a single coccoid member of the Cryptophyceae under the name of *Tetragonidium* and has very kindly furnished me with the drawings reproduced in fig. 219 E–J. This alga was found in moorland pools and appears as tetrahedral cells (12–18 μ in diameter) with cellulose walls, containing a brown lobed chromatophore (*c*) with a large pyrenoid (*p*). The assimilatory product is starch which appears not only around the pyrenoid, but also against the inner face of the chromatophore (fig. 219 E, *a*). The large nucleus (*n*) lies excentrically. Reproduction is effected by *Cryptochrysis*-like zoospores (fig. 219 G, H). On coming to rest they develop a thin envelope and soon acquire the tetrahedral form.

Status and Classification of the Cryptophyceae

While *Tetragonidium* clearly indicates a coccoid tendency on the part of the class, no other instances of the same kind have as yet come to light, nor have any filamentous types so far been discovered. Apart from the sexual reproduction recorded by Borzi in *Phaeococcus* (2b) there is no other record, although Pascher ((33) p. 51) casually mentions the occurrence of hologamy in Cryptomonadales.

The immediate affinities of this specialised class are obscure, but there are some striking resemblances with the Dinophyceae (Peridinieae, cf. p. 713) and perhaps a remote relation to the Phaeophyceae. There are also some points of resemblance to the Ochromonadeae ((26) p. 200), especially with such a form as *Wyssotzkia* (p. 517), but it is doubtful whether they imply any near affinity. Some relation to the Chlorophyceae is also possible, perhaps by way of the forms grouped by Korschikoff as Protochlorinae (cf. footnote 1 on p. 655).

The following is a synopsis of the classification:

I. *Cryptomonadales:*
  (*a*) *Cryptomonadineae:*
    1. *Cryptomonadaceae:* Chilomonas, Chroomonas, Cryptochrysis, Cryptomonas, Cyanomonas, Cyathomonas, Hillea, Rhodomonas.
    2. *Nephroselmidaceae:* Nephroselmis, Protochrysis, Sennia.
  (*b*) *Phaeocapsineae:*
    3. *Phaeocapsaceae:* Phaeococcus (?), Phaeoplax.
II. *Cryptococcales:*
    4. *Cryptococcaceae:* Tetragonidium.

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Protistol.* **2**, 148–69, 1923. **22*a*.** See No. 34 on p. 756 (Lauterborn, 1894). **23.** See No. 76 on p. 561 (Massart, 1920). **24.** Nägler, K. 'Ein neuartiger Typus der Kernteilung bei *Chilomonas paramaecium*.' *Arch. Protistenk.* **25**, 295–315, 1912. **25.** See No. 56 on p. 468 (Oltmanns, 1922). **26.** PASCHER, A. 'Ueber die Beziehungen der Cryptomonaden zu den Algen.' *Ber. Deutsch. Bot. Ges.* **29**, 193–203, 1911. **27.** PASCHER, A. 'Zwei braune Flagellaten.' *Ibid.* **29**, 190–2, 1911. **28.** PASCHER, A. 'Braune Flagellaten mit seitlichen Geisseln.' *Zeitschr. wiss. Zool.* **100**, 177–89, 1912. **29.** PASCHER, A. 'Cryptomonadineae', in *Süsswasserfl. Deutschlands, etc.* **2**, 96–114, 1913. **30.** See No. 132 on p. 57 (Pascher, 1914). **31.** See No. 97 on p. 561 (Pascher, 1917). **32.** PASCHER, A. 'Ueber das regionale Auftreten roter Organismen.' *Bot. 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Class VI. DINOPHYCEAE (PERIDINIEAE)

MODE OF OCCURRENCE

The members of this class play a very important rôle as plankton organisms, both in the sea and in fresh waters, although much greater diversity and elaboration of form is met with among the marine members. This is especially true of the Peridinian flora of warmer zones which differs very markedly from that of colder seas. While the North Atlantic, for instance, at times harbours a far greater bulk of Dinoflagellates than is to be found in the warmer parts of the oceans, the number of species involved is strikingly small compared with the Tropics and forms with a complex body-outline are rare or lacking (151). The highly elaborate Dinophysiales (p. 674) are essentially characteristic of tropical seas. The biggest rôle in practically all seas is played by the numerous species of *Ceratium* (69*a*), associated with which in northern waters are many species of *Peridinium*. According to Peters (134) the distribution of the diverse species of *Ceratium* is determined by temperature and the phosphate-content of the water. Many planktonic Dinophyceae are markedly phototactic and seek out those strata in which a light-intensity suitable to their requirements obtains (cf. also (39)). A number of Peridinieae favour estuaries and the coastal region (*Heterocapsa*, *Glenodinium foliaceum*) and at times occur there in enormous numbers (102). Freshwater Dinophyceae favour acid waters (62).

In the oceanic plankton the naked types abound, while the neritic plankton is far richer in armoured forms (cf. p. 692). In northern seas the maximum of Dinoflagellates follows upon that of the Diatoms (cf. (56) and p. 608). At the times of such maxima, both in the sea and in fresh water, these pelagic Dinophyceae may be represented in such numbers as to give a definite coloration of diverse tints (green, brown, etc.) to the water.[1] Some of the marine forms are phosphorescent, and in temperate waters the species most commonly responsible for this phenomenon is *Ceratium tripos*.[2] The cysts, often coloured red by haematochrome, have occasionally been observed to be the cause of red snow (159).

A small number of the marine Dinophyceae are inhabitants of the shore, causing a greenish brown discoloration of the sand at certain times. The forms involved are mainly species of *Amphidinium* and *Hemidinium*, intermingled with one or more species of *Gymnodinium*,

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[1] For the more important literature, see (59), (83) p. 242, (88) p. 44, (112), (113), (156), (165).

[2] See (25), (88) p. 52, (110*a*), (135), (140*a*), (142), (170).

Thecadinium, *Polykrikos*, *Exuviaella*, etc.(54, 55). The discoloration of the sand disappears shortly before it becomes covered by the rising tide and only reappears when the sand is again exposed. All of these sand-inhabiting forms are flattened and generally very mobile, while most of them are holophytic. For one of them (*Amphidinium Herdmani* Kof.) Bruce(12) has investigated the effect of the salt-content of the water on photosynthesis and distribution.

Among the flagellate Dinophyceae, and especially among the marine forms, a considerable number appear to lack chromatophores and to have adopted a holozoic (fig. 220 M) or parasitic mode of life (cf. pp. 686, 704). Such forms often show marked animal characteristics (nematocysts, ocelli), but it can hardly be doubted that they are derivative. Very few data as to the mode of feeding are available.

THE GENERAL CHARACTERISTICS OF THE CLASS

Whilst the majority of Dinophyceae are motile unicells, we owe to Klebs(73) and Pascher(115, 119) the discovery of a considerable number of types which show that here also evolution of a sedentary phase has not been lacking. Kofoid and Swezy's statement ((88) p. 109) that these forms present none of the Dinoflagellate characteristics is scarcely in harmony with the facts as detailed below (p. 706 et seq.).

The motile individual (fig. 220 A) is typically provided with two *flagella* arising close together, but differing in structure and orientation. The one directed transversely (*t*) is band-shaped and exhibits an undulatory movement, the other directed longitudinally and posteriorly (*l*) is thread-like or sometimes also band-shaped(38); both are probably concerned in forward progression (cf. p. 682). In the vast majority of cases these flagella arise from the ventral surface through definite pores (fig. 220 A) and only in a few possibly primitive forms from the anterior end of the individual (cf. p. 671). They are usually partly or entirely located within special transverse (*g*) and longitudinal furrows (*s*) on the surface of the cell.

According to Hall(51, 52) each flagellum in *Ceratium hirundinella* and *Oxyrrhis marina* terminates in a basal granule just within the surface; from each granule a rhizoplast extends to an extranuclear centrosome adjacent to the nucleus (fig. 220 F, G). In cell-division the centrosome divides, each half remaining connected with a rhizoplast and a flagellum, while the two centrosomes are temporarily united by a thread (centrodesmose, fig. 220 E, *d*). Two new flagella, completing the equipment for the two daughter-individuals, arise during nuclear division. In *Oxyrrhis* one of the two centrosomes is joined to the nucleolus by an intranuclear rhizoplast (fig. 220 E) and the same is recorded by Jollos(70) for other Peridinieae. Reichardt(141) also records centrosomes in *Gloeodinium*.

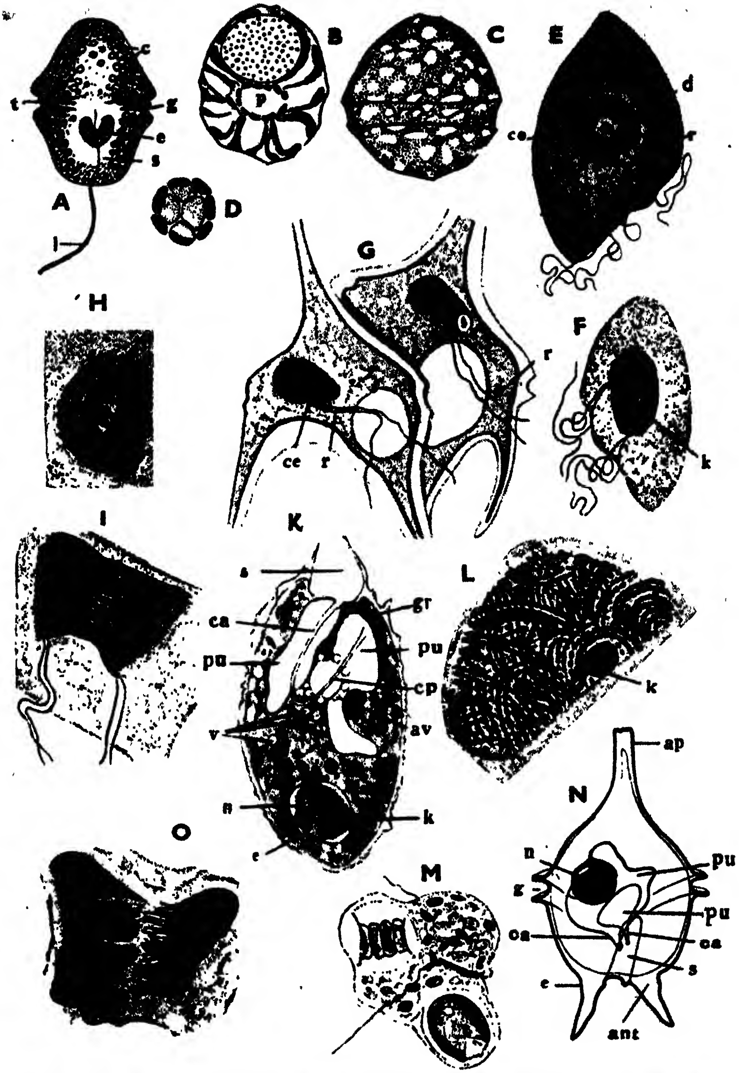

Fig. 220. General characteristics of the Dinophyceae. A, *Glenodinium cinctum* Ehrenb., motile individual. B–D, *Peridinium umbonatum* Stein var.; B, optical section; C, surface view; D, pyrenoid with envelope of starch-grains. E, F, *Oxyrrhis marina* Duj., successive stages in nuclear and cell-division; E, late prophase; F, late metaphase. G–I, L, O, *Ceratium hirundinella* O. F. M.; G, late stage of division; H, early prophase; L, early

The greatest diversity exists in the character of the *cellular envelope* which consists in the main of cellulose (105)[1] and upon whose features the classification is largely based. In some of the simpler forms a membrane is apparently lacking, but in the more advanced types it attains to a degree of complexity only paralleled among the Bacillariophyceae (cf. figs. 229, 230). In many of the more specialised forms this envelope is of considerable thickness. It is often produced externally into processes (fig. 220 G, N), wings, etc., that give the individuals a characteristic shape and are no doubt in most cases of the nature of planktonic adaptations (cf. especially figs. 223, 224). As far as present knowledge goes there is a delicate internal membrane upon which the main portion of the envelope is deposited (32, 105). In many forms the presence of pores (fig. 230 G, J) or poroids (pits, cf. p. 578) has been demonstrated ((152) p. 20, (154)). Schütt held that, as he believed to be the case in Diatoms, cytoplasm passed out through the pores to form a delicate extramembranous layer, responsible for the development of the diverse centrifugal outgrowths of the membrane, as well as serving for metabolic exchange with the surrounding medium (cf. also (89)). Mangin (108) is of the opinion that, in addition, a formation of processes from the interior of the cell is possible.

The *protoplast*[2] commonly consists of an outer denser and more or less granular region harbouring the chromatophores in the holophytic forms, and an inner portion that contains nucleus and vacuoles (150). In the neighbourhood of the flagellar pores the cytoplasm is more fluid and mobile and readily puts forth pseudopodia here (39, 169). Busch (13) also records a formation of delicate rhizopodia from all points of the surface in a marine *Gymnodinium* and this no doubt is not uncommon in the naked types (cf. also (39)). Eye-spots have so far only been observed in the freshwater forms (fig. 220 A, *e*), but some of the marine types possess elaborate ocelli (p. 685) which are possibly their equivalents.

[1] Pearsall (130) finds that in *Ceratium hirundinella* the cellulose reaction is obtained with increasing difficulty as the season advances.

[2] In very many of the marine Dinophyceae little or nothing is so far known of the structure of the cell-contents owing to the difficulties of adequate preservation.

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metaphase; I, metaphase plate; O, end of metaphase. K, *Phalacroma* sp., showing vacuolar system. M, Undetermined member of Gymnodiniaceae showing holozoic nutrition. N, *Peridinium Steinii* Joerg. *ant*, antapical and *ap*, apical horns; *av*, accessory vacuoles; *c*, chromatophores; *ca*, canal of pusule; *ce*, centrosome; *cp*, collecting pusule; *d*, centrodesmose; *e*, stigma; *g*, girdle (transverse furrow); *gr*, granules on pusule-wall; *k*, caryosome; *l*, longitudinal flagellum; *n*, nucleus; *p*, pyrenoid; *pu*, sack pusule; *r*, rhizoplast; *s*, sulcus (longitudinal furrow); *t*, transverse flagellum; *v*, vacuoles. (A after Schilling; B–D after Geitler; K, N after Haye; M after Pascher; the rest after Hall.)

The *chromatophores*, which are very delicate and under abnormal conditions readily alter their shape or undergo disorganisation, appear usually to be numerous and more or less discoid in form, although spindle- or band-shaped chromatophores have also been recorded; not uncommonly they exhibit a radial arrangement in the cells. Among the primitive members of the Desmokontae there are generally one or two large chromatophores, while according to Geitler (46) some species of *Peridinium* (e.g. *P. umbonatum* var.) have a single richly lobed axile chromatophore (fig. 220 B), the lobes radiating from a central point and spreading out parietally to form an anastomosing network (fig. 220 C). Similar chromatophores are recorded by Zimmermann (172) in *Amphidinium*.

Pyrenoids occur commonly in Desmokontae, but of their distribution in other Dinophyceae little is known. Schütt ((152) p. 93) records a pyrenoid in *Heterocapsa*, while Geitler and Zimmermann describe a single central pyrenoid in the lobed chromatophores of *Peridinium* and *Amphidinium* just referred to (fig. 220 B, *p*), that of the former being surrounded by a sheath of polygonal starch-grains (fig. 220 D). The algal members of the class appear to lack pyrenoids.

The chromatophores exhibit varied pigmentation, though shades of dark yellow and brown are the commonest. According to Schütt three pigments can be extracted from them ((149), (152) p. 62),[1] viz. the water-soluble brownish red phycopyrrin, the dark red peridinin, and the yellowish green chlorophyllin, the two latter soluble in alcohol; the different tints of these organisms are stated to be due to the varied representation of these pigments. Kylin (91), working with a species of *Peridinium*, denies the presence of a water-soluble pigment, but concludes that there are three carotinoid pigments—carotin, phylloxanthin, and peridinin—the latter being the cause of the brown coloration. A few blue-green forms are known (e.g. *Gymnodinium aeruginosum*, *G. coeruleum* (29, 45)) which are said to contain phycocyanin.

Reserve-food is stored as starch and fat, the latter being usually the only recognisable substance in the marine forms and often being brilliantly coloured (yellow or red). While the majority of freshwater forms possess chromatophores, these appear to be lacking in a large percentage of the marine motile types (e.g. many species of *Gymnodinium* and *Peridinium*). In these the cytoplasm is commonly vividly coloured (red, yellow, etc.), especially in species frequenting warmer seas, although a striking example of such a coloured form (*Gyrodinium britannica* (95)) is found in the waters round Plymouth. Evidence of holozoic nutrition is to be found in the presence of vacuoles containing food-bodies, and it seems that some of the holophytic forms may also occasionally ingest food in this way (see (88) p. 46, (95) p. 4; also p. 704).

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[1] These are commonly known collectively as pyrrophyll; cf. the criticisms of Czapek (24).

According to Schütt ((151) p. 28, (152) p. 78) leucoplasts may be present in the cells of the colourless forms.

The *nucleus* is generally large and conspicuous,[1] the outer nucleus either containing numerous fine granules (fig. 220 K) or commonly exhibiting numerous very fine tangled moniliform threads containing the chromatin (fig. 220 G); the latter type is especially distinctive of many of the Dinoflagellata. One or more nucleoli may be present which disappear during division, except in *Oxyrrhis* (51) and *Gyrodinium fucorum* (70). Nuclear division is characterised by the numerous elongate chromosomes (fig. 220 I, O) which are often prominently beaded and are sometimes clearly recognisable already in the early phases (fig. 220 H, L). In *Oxyrrhis* they show a radial arrangement in the late prophase (fig. 220 E). No evident spindle-fibres are formed during mitosis.

The investigations have largely dealt with the nucleus of species of *Ceratium*, and there have been diverse differences of interpretation. It remains doubtful (9) whether a granular distribution of the chromatin is not in all cases characteristic of the resting nucleus. In *Ceratium hirundinella*, Hall (52) describes the early prophase as showing only a few short scattered chromosomes, but in later stages they become much longer and exhibit a coiled arrangement within the nucleus (fig. 220 L). Both in this species and in *Oxyrrhis* (51) the chromosomes split lengthwise in the early metaphase and collect at the equator as pairs of daughter-chromosomes joined at their ends. Earlier workers (8, 33, 93, 147) had affirmed a transverse division of the chromosomes at this stage, but according to Hall this transverse division merely completes the separation of the daughter-chromosomes formed by the longitudinal split and does not effect transverse division of whole chromosomes.

Oxyrrhis marina (30, 51) is peculiar in the fact that the single nucleolus persists during division and becomes drawn out in the same way as in Euglenineae (fig. 220 F). According to Jollos ((70) p. 184) the caryosome of *Gyrodinium fucorum* contains a centrosome that divides with it, the two parts remaining connected by a delicate bridge (centrodesmose) (cf. however (5*a*) p. 336). Marked centrospheres have also been recorded in some of the parasitic forms (19).

Large definite *vacuoles* (*pusules*)[2] are very characteristic of Dinoflagellates (fig. 220 K, N), though so far they have only been observed in the marine forms ((53), (88) p. 22, (150), (152) p. 45). These pusules (sack-pusules of Schütt) may be spherical, but commonly they are elongate or even bilobed structures which exhibit only slight contraction and are bounded by a well-defined vacuolar membrane. Very

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[1] For the more important literature, see (5*a*) p. 98, (8), (9), (30), (33), (41), (51), (52), (70), (73) p. 416, (88) p. 18, (93), (147).

[2] By vital staining with Congo red Dangeard (27) demonstrated the presence of numerous small vacuoles in a marine *Ceratium*; these, however, are not of the nature of pusules.

frequently there are two of them which may be of different shape (fig. 220 K, N, *pu*) and they are sometimes joined by a fine canal. They are largest, according to Kofoid and Swezy (88), in the forms with a well-developed envelope. Each pusule communicates with the exterior by a delicate canal which opens into one or other of the pores through which the flagella emerge (fig. 220 N, *ca*). In some cases in addition to the sack-pusules there is a so-called *collecting pusule* (fig. 220 K, *cp*) which is itself surrounded by a ring of accessory vacuoles (*av*) of smaller size communicating with the collecting pusule. The fluid within the pusules is usually coloured rose or salmon pink. According to Kofoid (78) these vacuoles do not excrete, but absorb liquid from the exterior. He believes (cf. (88) p. 49) that this helps the saprophytic forms in the obtaining of nutriment, although no nutritive particles have been demonstrated within the pusules. He points out that they are most strongly developed in the armoured Peridinieae among the colourless saprophytic forms ((78) p. 35). This view has not, however, met with general acceptance (cf. (53)), and it still remains to be shown that these structures are not excretory like similar contrivances in other classes.

Pascher (115, 119) separates from the main series of the Dinophyceae a group, the Desmokontae, which show on the whole a more primitive organisation. For the remainder he uses the name Dinophyceae, uniting these two groups, together with the Cryptophyceae, in a division Pyrrophyta. To me, however, it appears more appropriate to designate the whole class of Peridinian forms by the name of Dinophyceae and to distinguish among them two groups, the Desmokontae and the Dinokontae (Pascher's Dinophyceae). Whether the available evidence is sufficient to unite these two groups with the Cryptophyceae in a common division will be discussed at the end of this section.

A. *DESMOKONTAE*

The Desmokontae, which with a solitary exception comprise only motile unicells, are a less specialised series than the Dinokontae, although in their more advanced members they exhibit fundamental features of the Peridinian organisation. The envelope, however, never appears to consist of the complex series of plates that is characteristic of the higher Dinoflagellata. The simplest members, the Desmomonadaceae, exhibit none or few of the complexities of other Dinophyceae and probably give us a certain picture of the prototypes of the whole class.

THE FAMILY DESMOMONADACEAE (DESMOMONADALES)

Pascher's *Desmomastix* ((145) p. 7), found in fresh water, has naked ellipsoidal cells (fig. 221 A), circular in cross-section (fig. 221 B), with two apically inserted somewhat band-shaped flagella, one of

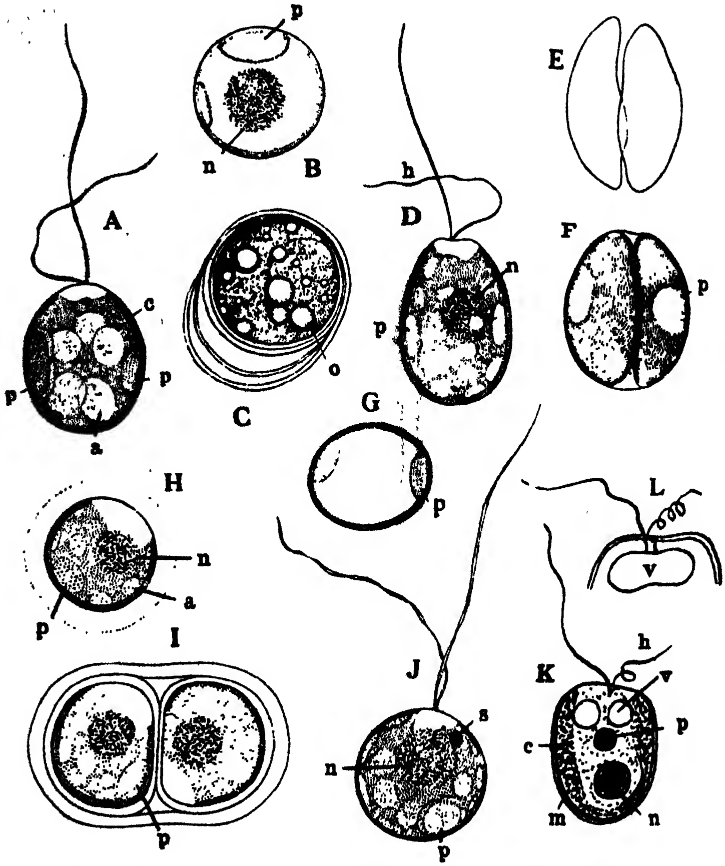

Fig. 221. The family Desmomonadaceae. A–C, *Desmomastix globosa* Pascher; B, optical transverse section; C, cyst. D–G, *Pleromonas erosa* Pascher; E, the two halves of the membrane; F, division; G, optical transverse section. H–J, *Desmocapsa gelatinosa* Pascher; H, single cell; I, division; J, swarmer. K, L, *Haplodinium antjoliense* Klebs. *a*, starch-grains; *c*, chromatophore; *h*, horizontal flagellum; *m*, membrane; *n*, nucleus; *o*, oil; *p*, pyrenoid; *s*, stigma; *v*, vacuole. (K, L after Klebs; the rest after Pascher from Schiller.)

which exhibits undulatory movements. There are two large lobed chromatophores (*c*) occupying most of the periphery of the cell and containing each an excentric pyrenoid (*p*) which projects markedly on the inner surface (fig. 221 A, B); starch in the form of large grains (*a*) constitutes the assimilatory product. The large central nucleus (*n*) exhibits a structure consisting of numerous fine threads, as in many Dinophyceae. Multiplication takes place by longitudinal division during movement, while cysts (fig. 221 C) with a stratified envelope of cellulose and containing large oil-drops are also known.

In the marine *Pleromonas* ((145) p. 8) (fig. 221 D) there is a delicate cellulose-envelope which, when the protoplast is caused to swell, ruptures along the antero-posterior plane into two irregular halves (fig. 221 E). The anterior end of the organism is slightly emarginate and from its middle arise two band-shaped flagella, one of which (*h*) is directed horizontally and shows irregular undulations. There is a single brown, somewhat perforated chromatophore, apparently occupying nearly the whole periphery of the cell and containing two bulging pyrenoids (fig. 221 D, G, *p*); the assimilatory products take the form of solid granules. Division occurs after withdrawal of the flagella (fig. 221 F). In neither of these genera have contractile vacuoles been recognised.

The third member of the family, *Haplodinium* (fig. 221 K), was described in 1912 by Klebs (73) from brackish water in Java and has not since been observed. Its broadly ovate, somewhat flattened cells, provided with a firm cellulose membrane (*m*), possess a truncated, slightly oblique front end with a faint incision from which the two unequal flagella arise; one of these is stretched out anteriorly, while the other (*h*) is coiled in corkscrew fashion and directed more horizontally (cf. also fig. 221 L). There are two plate-like yellowish chromatophores (*c*), each with a projecting pyrenoid. A large nucleus (*n*) lies at the back and two large (contractile?) vacuoles (*v*) are located at the front end; the vacuoles can flow together to form a single sac-shaped structure communicating by a canal with the surface of the cell (fig. 221 L).

The significant feature in the organisation of these three genera is the difference in the two flagella which is of the same nature as in the more advanced Dinophyceae; this is especially marked in *Pleromonas* and *Haplodinium* where the undulating flagellum shows a marked tendency to be directed horizontally. These forms should be compared with *Entomosigma* (p. 689). Pascher ((145) p. 11) has also briefly described a palmelloid member of the family, *Desmocapsa*. It occurred attached to marine Algae as minute mucilaginous clumps containing round brown-coloured cells with the typical large nucleus and a single chromatophore with a pyrenoid (fig. 221 H, I). The cells multiply by division and may also escape as spherical swarmers (fig. 221 J) with two apical band-shaped flagella and a pronounced eye-spot (*s*). Cysts with a stratified cellulose-envelope are also recorded.

THE FAMILY PROROCENTRACEAE (THECATALES)

A rather more specialised family, clearly related to the Desmomonadaceae, are the marine Prorocentraceae, in which the cell-membrane is composed of two distinct halves, the suture (fig. 222 A, D, H, *s*) joining them running from the anterior to the posterior end[1] (cf. *Pleromonas*). The cells are commonly strongly flattened parallel to this suture, although this is not very pronounced in *Exuviaella*

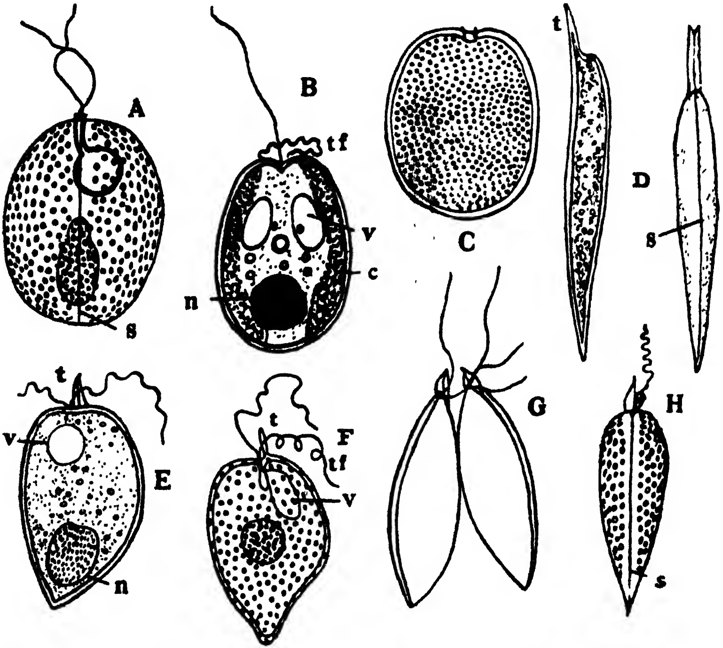

Fig. 222. The family Prorocentraceae. A, B, *Exuviaella marina* Cienk. C, *E. compressa* Ostenf. D, *Prorocentrum rostratum* Stein, the right-hand individual seen from the narrow side. E–H, *P. micans* Ehrenb.; G, division; H, individual seen from the narrow side. *c*, chromatophore; *n*, nucleus; *s*, suture; *t*, tooth; *tf*, transverse flagellum; *v*, vacuole. (A, H after Schütt; B after Klebs; D after Stein; F after Kofoid & Swezy; the rest after Lebour.)

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[1] This appears to be a more justifiable orientation of the individual (cf. (133)) than that adopted by Schütt (153) and Lindemann (102) who regard the suture as running transversely.

(fig. 222 A), so that the two halves (valves) of the membrane are often like two watch-glasses (fig. 222 H). The two flagella emerge apically through a pore which occurs as an emargination in one of the valves of which the wall is composed (fig. 222 A); in some cases, however, there are separate pores for the two flagella. In *Exuviaella* (72, 73, 94, 136, 137) there are commonly minute teeth-like prominences on either side of the flagellar aperture (fig. 222 A), while in *Prorocentrum* (6, 121, 137, 157) there is often a single apical tooth which is frequently very prominently developed and occupied by cytoplasm (fig. 222 D, E, *t*). The orientation of the flagella is very similar to that found in *Haplodinium* (fig. 222 B, F); one, which is thread-like and directed anteriorly, pulls the individual forwards, whilst the second band-shaped undulatory flagellum (*tf*) swings transversely about it and causes a rotation of the individual.

The valves are mostly provided with numerous scattered pores which are usually lacking in the neighbourhood of the suture (cf. fig. 222 A, H). As a general rule there are two brownish yellow chromatophores, apposed to the two valves (fig. 222 B) and in *Exuviaella* usually harbouring a pyrenoid. A few species of *Prorocentrum* have a number of small chromatophores. The nucleus is lenticular or commonly kidney- or even V-shaped. One or two usually spherical vacuoles lie near the flagellar pore and communicate with it by definite canals (fig. 222 A, B, F). In *Exuviaella* the cells are in most cases rounded at both ends, whilst those of *Prorocentrum* are generally markedly pointed at the posterior extremity (fig. 222 E, F); the extreme is reached in such a form as *P. rostratum* (fig. 222 D). Some species of *Prorocentrum* are phosphorescent, while *Exuviaella marina* is a common inhabitant of the sand in the littoral zone.

Multiplication of these forms takes place by longitudinal division (fig. 222 G), the daughter-individuals retaining one valve of the parent and forming the second afresh (cf. Diatoms). An escape of the protoplast from the membrane has been observed in *Exuviaella*. Schiller ((145) p. 12) also mentions the probability of the escape of the protoplast as a swarmer and of division occurring in this condition.

THE DINOPHYSIALES

The most advanced members of the Desmokontae are to be found among the Dinophysiales[1] with a number of families. The envelope here, while again consisting of two laterally disposed halves joined by an antero-posterior suture (fig. 223 C, *su*), is provided with transverse and longitudinal furrows within which the respective flagella lie (fig. 223 G, *s*, *g*). The latter emerge through a common pore within

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[1] See (6), (86), (102), (129), (145), (157).

the longitudinal furrow. The side of the individual bearing the longitudinal furrow or *sulcus* is spoken of as the ventral side (fig. 223 G), while the opposite (fig. 223 A) is the dorsal side. The part of the wall above the transverse furrow constitutes the *epivalve* (*e*), the part below the *hypovalve* (*h*). The transverse furrow (*girdle*) is usually located close to the anterior extremity, so that the flagellar aperture is not far from that end (fig. 223 A, G), and the edges of the furrow are frequently developed as pronounced wings; similar wings are often to be found bounding the longitudinal furrow (cf. fig. 223 D–F, *w*). Flattening of the individual, as in the Prorocentraceae, is frequent (e.g. *Dinophysis*, fig. 223 C, C′; *Ornithocercus*, fig. 224 H). The membrane is probably in most, if not in all cases, composed of a number of plates, and Entz (31) has drawn attention to the homologies with the species of *Ceratium* in this respect.

The Dinophysiales are a highly evolved group of marine plankton forms, mainly found in tropical seas, and many of their members show far-going adaptation to the floating habit. Typical representatives are to be seen in *Phalacroma* (fig. 223 A, D) and *Dinophysis* (fig. 223 B, C, C′). The epivalve (*e*) is small, while the hypovalve (*h*) is large and commonly more or less conical. The two are separated by the transverse furrow or girdle (*g*), whose margins are prominently winged. In *Phalacroma* (fig. 223 A) these wings project more or less horizontally, but in *Dinophysis* (fig. 223 B) they are directed anteriorly and appear as two funnel-shaped collars encircling the front end of the individual. The longitudinal furrow (sulcus), which coincides with the suture joining the two halves of the membrane, commences at the transverse furrow and extends some distance towards the posterior end (fig. 223 G, *s*). Its edges are developed as vertical offstanding wings, similar to sails, that of one edge being considerably larger than that of the other and being strengthened by three radiating spine-like ridges (fig. 223 B, D, E, *w*). The furrows are in the main indicated only by the wings and do not constitute any evident depression in the membrane. In some forms there is also a posterior wing developed in the plane of the suture (fig. 223 I)

The membrane is often areolated with a prominent pore in the middle of each areola (fig. 223 A–D; cf. also fig. 230 J). The transverse flagellum (*t*) is altogether confined to the furrow, whilst the posterior part of the longitudinal one (fig. 223 B, E, F, *l*) projects from the longitudinal furrow, features in which these forms altogether resemble the typical Dinoflagellata. A considerable number of the species of the two genera under discussion appear to be colourless, such forms often having reddish or yellowish green cytoplasm. There are two large pusules of very diverse shape (cf. fig. 220 K), the one near the transverse furrow, the other in the posterior part of the cell

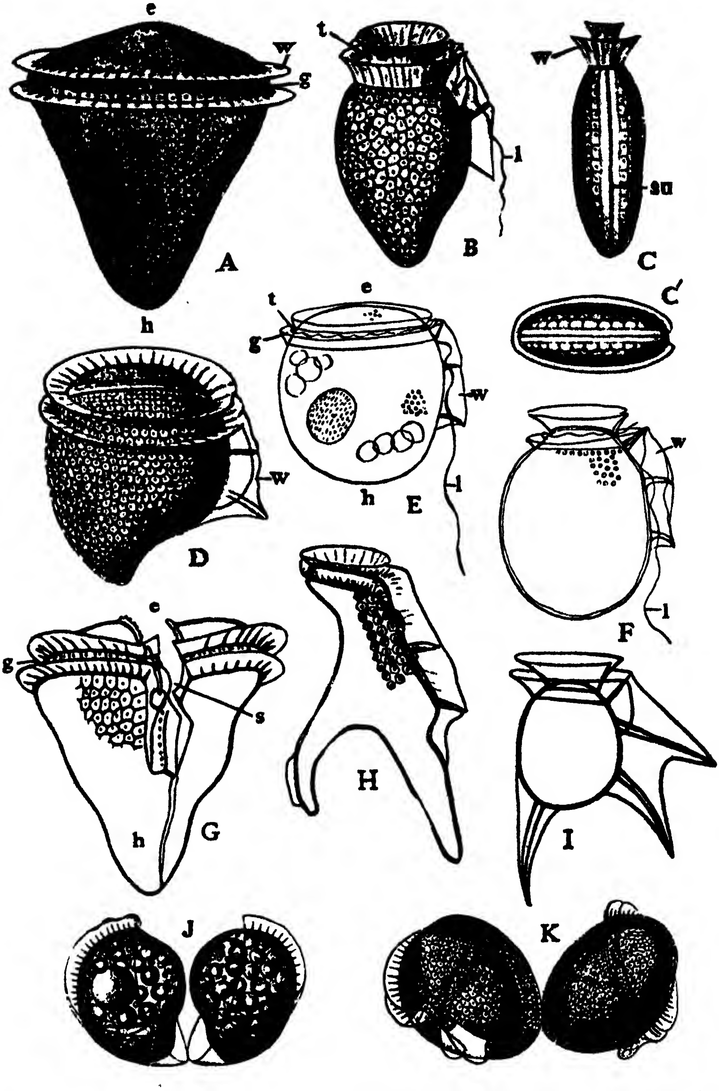

Fig. 223. Dinophysiales. A, D, G, *Phalacroma mitra* Schütt; A, from the dorsal, D from the right-hand, and G from the ventral sides. B, C, C′, *Dinophysis acuta* Ehrenb.; B from the right-hand, C from the dorsal sides; C′ in section. E, *Phalacroma rotundatum* (Clap. et Lachm.) Kof. et Mich.,

In the elaborate *Ornithocercus*(151, 157) (fig. 224 B) the transverse furrow (*g*) is very broad, and wider on the dorsal than on the ventral side; the epivalve is reduced to two small plates united along the longitudinal suture. The winged edges of the transverse furrow are strongly developed, the anterior one forming a large funnel-shaped structure; both have numerous stiffening ridges which in some species are connected by a system of reticulate veins (fig. 224 H). These two wings enclose a wide annular space which often contains small brown bean-shaped cytoplasmic masses (phaeosomes) of problematical nature. The two wings of the longitudinal furrow, as in the two genera previously discussed, are unequally developed, the larger often extending to the posterior extremity of the individual, its anterior edge being fused with the posterior wing of the transverse furrow (fig. 224 B). This larger wing, moreover, is fused with the posterior wing which latter often extends well over on to the dorsal surface. This elaborate sail-like structure is stiffened by variously developed radial ridges. Chromatophores have not been recorded.

The most remarkable form is attained by *Amphisolenia*(157), in which the individual has a narrow needle-like shape (fig. 224 A) and is not uncommonly more or less curved. Between the somewhat enlarged main body and the almost apical transverse furrow (fig. 224 D, G, *g*), which is disposed somewhat obliquely, a narrow neck (*n*) is intercalated, while the posterior end of the individual is drawn out into a more or less elongate process; in some species this posterior prolongation is branched, being provided with one or more ventral outgrowths. The longitudinal furrow continues only as far as the main body (fig. 224 D, *s*) and the flagellar aperture (*fp*) is located at its lower end. The transverse flagellum extends from here to the transverse furrow and encircles the latter in the usual way; the longitudinal flagellum has not yet been certainly recognised. The wings (two transverse and two equally developed longitudinal ones) are less markedly differentiated than in the genera previously discussed and are not always provided with stiffening ridges. The membrane is usually smooth.

Of the reproduction of the Dinophysiales little is known(31, 124, 152, 158). In several cases multiplication of the individuals by oblique longitudinal division has been observed, in which case the two halves of the membrane separate, the missing half being formed anew (figs. 223 J, K; 224 C).

from right-hand side. F, *Dinophysis recurva* Kof. et Skogsb., from right-hand side. H, *D. miles* Cleve. I, *D. Schüttii* Murr. & Whiting. J, K, *Phalacroma vastum* Schütt, division. *e*, epivalve; *g*, girdle (transverse furrow); *h*, hypovalve; *l*, longitudinal flagellum; *s*, sulcus (longitudinal furrow); *su*, suture; *t*, transverse flagellum; *w*, wing. (E, F after Lebour; H after Schiller; I after Kofoid & Skogsberg; the rest after Schütt.)

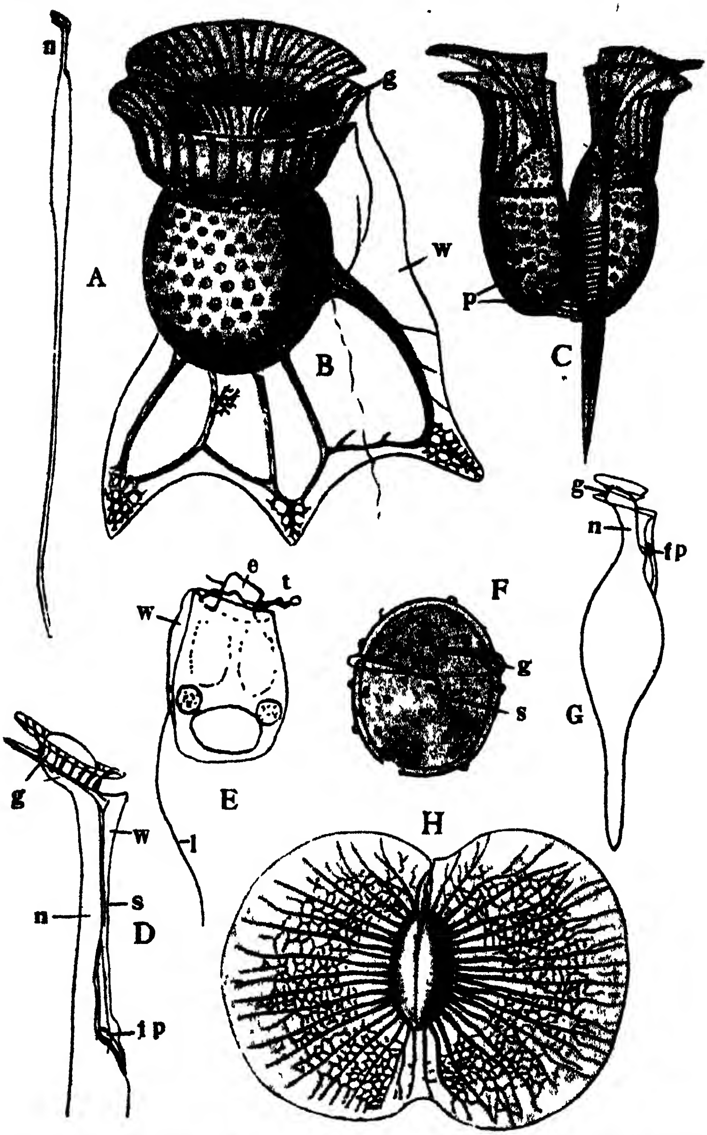

Fig. 224. Dinophysiales. A, D, *Amphisolenia spinulosa* Kof.; D, enlarged anterior end. B, C, H, *Ornithocercus magnificus* Stein; B, from right-hand

The relation of the group to other Dinophyceae is variously interpreted. Among the species of *Prorocentrum* there are several in which the flagellar pore has shifted somewhat on to the ventral surface and in such the tooth follows suit. This tendency is regarded by Schiller ((145) p. 47) as pointing the way to the Dinophysiales which the Prorocentraceae also resemble in the antero-posterior division of the membrane into two halves, the compression of the cell along this plane, the more or less band-shaped transverse flagellum, and the occurrence of curious much enlarged cells which are possibly reproductive. If I understand Schiller rightly, he suggests that the dorsal tooth of *Prorocentrum* has in the Dinophysiales enlarged to form the epivalve, while the slight depression from which the flagella often arise in the former genus and which thus comes to lie on the ventral surface has widened to form the transverse furrow. As a transitional form between the Prorocentraceae and the Dinophysiales he regards *Palaeophalacroma* (fig. 224 F) where the transverse furrow (*g*) is represented only by a horizontal ridge, whilst the longitudinal furrow (*s*) is very narrow without marginal wings.

Kofoid and Skogsberg (86), on the other hand, derive the Dinophysiaceae from *Amphidinium* among Gymnodinioideae (p. 683) by way of the genus *Thecadinium*. This includes two sand-inhabiting forms, originally described as species of *Phalacroma* (55), with a very simple structure. The species of *Thecadinium* resemble *Amphidinium* in the possession of a soft envelope and a very small epivalve (fig. 224 E, *e*), but differ in the lateral compression of the body and the presence of a longitudinal suture. The latter feature, which is characteristic of the Dinophysiales, seems to mark off *Thecadinium* sharply from the Dinokontae. Moreover, the simple structure of these forms, as Schiller points out, may well be a result of their unusual habitat.

B. *DINOKONTAE*

The Dinokontae include the main line of development of the Dinophyceae and show considerable homogeneity. Whether, in conformity with the view of Kofoid and Skogsberg just discussed (cf. also (102)), the Dinophysiales should be included here as a specialised series must for the present remain an open question. None of the forms

side; C, stage in division; H, seen from posterior end. E, *Thecadinium ebriolum* Kof. et Skogsb. F, *Palaeophalacroma verrucosum* Schill. G, *Amphisolenia inflata* Murray & Whiting. *e*, epivalve; *fp*, flagellar pore; *g*, girdle (transverse furrow); *l*, longitudinal flagellum; *n*, neck; *p*, pore; *s*, sulcus (longitudinal furrow); *t*, transverse flagellum; *w*, wing. (A, D after Kofoid; B, H after Schütt; C after Stüwe; E after Herdman; F after Schiller; G after Kofoid & Skogsberg.)

considered in the following possess a membrane composed of two halves separated by an antero-posterior suture, although all show essentially the same furrow-structure as the Dinophysiales. The motile members exhibit a great range of differentiation and are classed as

Order I. *DINOFLAGELLATA*

The individuals are commonly more or less subcircular, ovoid or pyramidal in outline (fig. 225 A, C) and are often flattened dorsiventrally so that the end-view appears more or less subelliptical (cf. figs. 229, 230). In many cases they are provided with a well-marked envelope consisting largely of cellulose (105, 108), and in the advanced forms composed of a definite number of regularly arranged and often elaborately sculptured plates (cf. figs. 229–31). In a considerable number of genera of the Gymnodinioideae, however, a membrane is apparently lacking or indistinct. The protoplast, which is bounded by a firm plasma-membrane, is provided with two furrows, the one (girdle) transverse and the other (sulcus) longitudinal, and this structure, which is eminently characteristic of all Dinoflagellata, is exhibited also by the overlying envelope when that is present (fig. 225 A, F).

The transverse furrow is usually well marked and, with few exceptions (e.g. *Hemidinium*, fig. 225 B), completely encircles the cell, separating the *apical* half (epivalve) which is directed forwards during movement from the *antapical* half (hypovalve). The longitudinal furrow, which is not uncommonly rather broad and often less distinct, lies on the ventral flank of the usually flattened cell. It is often confined to the antapical half (fig. 225 A, *s*), opening into the transverse furrow (*g*) at its upper end, or it may continue across the latter for a varying distance into the apical half (fig. 225 F). In *Gonyaulax* (fig. 225 D) it almost reaches the anterior extremity, but this is unusual.

In some cases the transverse furrow follows a more or less horizontal course, the portions to right and left of the sulcus being at practically the same level (fig. 225 A, C). There is, however, often a slight spiral trend (fig. 225 F, I) and in *Gyrodinium* (fig. 225 E), for example, the transverse furrow appears as a steep spiral and the two sections of it visible on the ventral surface are far apart, though linked by a part of the longitudinal furrow, often known as the *intercingular area* (*s*). In most cases the spiral transverse furrow descends to the left (as seen from the dorsal surface),[1] the left-hand part on the ventral surface being nearer the apex than the right-hand part (fig. 225 F).

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[1] It is usual to describe the cell of the Dinoflagellata with respect to its aspect from the dorsal surface, the apical pole being directed forwards.

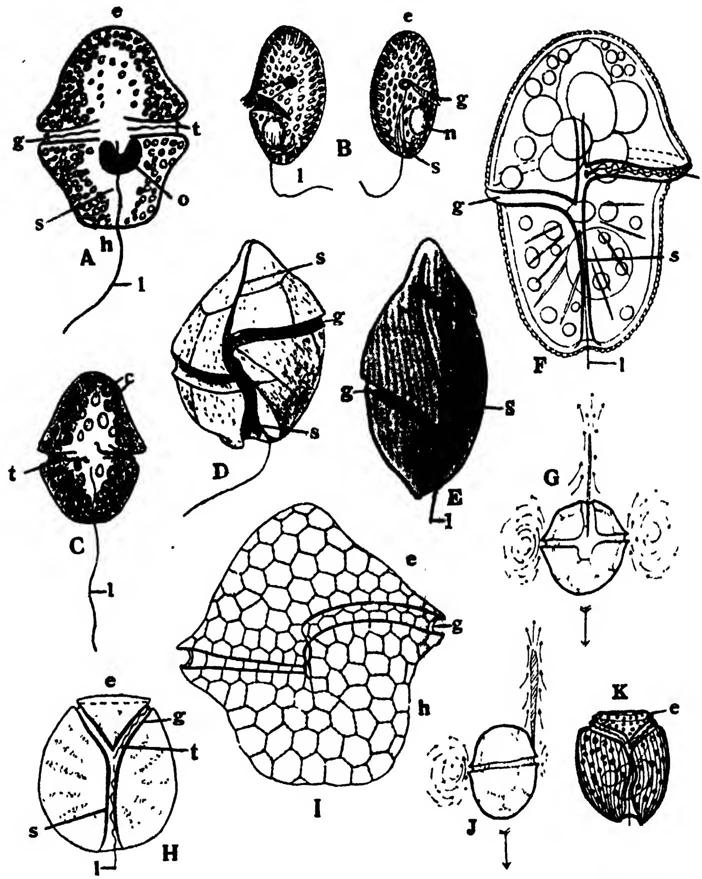

Fig. 225. Dinoflagellata. A, *Glenodinium cinctum* Ehrenb. B, *Hemidinium nasutum* Stein, on the left from the dorsal, on the right from the ventral surface. C, *Gymnodinium aeruginosum* Stein. D, *Gonyaulax fragilis* (Schütt) Kof., ventral surface. E, *Gyrodinium spirale* (Bergh) Kof. et Swezy. F, *Gymnodinium pachydermaticum* Kof. et Swezy. G, J, *Peridinium cinctum* Ehrenb., G from the ventral, J from the dorsal surface; the small arrows indicate the direction of the currents of sepia-particles caused by the movements of the flagella, the large ones the direction of movement. H, *Amphidinium Herdmani* Kof. et Swezy. I, *Gymnodinium hiemale* Wolosz. K, *Amphidinium truncatum* Kof. et Swezy. *c*, chromatophore; *e*, epivalve; *g*, girdle; *h*, hypovalve; *l*, longitudinal flagellum; *n*, nucleus; *o*, stigma; *s*, sulcus; *t*, transverse flagellum. (A, C after Schilling; B after Lemmermann; D, E after Schütt; G, J after Metzner; I after Woloszyńska; the rest after Kofoid & Swezy.)

But the opposite condition (winding to the right) also occurs, and among the species of *Peridinium* there are some in which the furrow descends to the left and some in which it descends to the right.

In the majority of Dinoflagellata the two flagella emerge through separate apertures in the membrane, often close together at the point where the furrows meet, but sometimes (fig. 225 F; *Gyrodinium*, fig. 225 E) more or less markedly removed from one another; in the Peridinioideae they pass out through a common slit-shaped aperture (fig. 230 A, *fp*). The band-shaped transverse flagellum, according to Kofoid and Swezy ((88) p. 11; cf. also (38)), consists of a deeply staining fibril with a one-sided wing, somewhat longer than the fibril "and thrown into ripples or folds of wider amplitude than the fibril". When the individual is viewed from the ventral surface with the apical half directed forwards, this transverse flagellum extends from its point of origin to the right along the transverse furrow and, passing round the dorsal surface, reappears again on the left-hand side to terminate close to its starting-point (fig. 225 A, C, D). It thus encircles the individual, but is confined to the furrow and does not project in any way. The second flagellum is a fine thread (sometimes also band-shaped), often considerably longer than the body of the cell, and is directed backwards during movement; its proximal portion lies in the longitudinal furrow, but the greater part projects into the surrounding water. Ohno (114) has described a *Gymnodinium* with two longitudinal flagella.

According to Metzner and Peters ((110), (133); cf. also (38)) both flagella are concerned in movement. The transverse flagellum which is coiled in a close spiral exhibits, as in the Desmokontae, undulating movements and, according to Metzner, causes a direct forward propulsion whilst at the same time conditioning a rotation of the individual. The longitudinal flagellum, which likewise shows undulatory movements, swings in a narrow orbit lying mainly in the dorsoventral plane and gives a marked forward push, whilst simultaneously acting as a rudder (cf. fig. 225 G, J). According to Lindemann (101) both flagella are about equally responsible for movement in *Hemidinium*, and loss of the one or the other does not appreciably alter the movement, except that under these circumstances the anterior end of the individual exhibits a slight circular motion.

Pascher (118) has described a remarkable colourless form, *Clipeodinium*, in which the longitudinal flagellum is lacking, while the antapical half of the body is developed in the form of a hollow cone. Forward progression is in this case brought about by rhythmic contraction and expansion of the medusa-like protrusion of the antapical half (cf. *Medusochloris*, p. 88).

(b) THE UNARMOURED FORMS (GYMNODINIOIDEAE)

The Free-living Types

The simplest members of the Gymnodinioideae are found among the Gymnodiniaceae in the genus *Gymnodinium* (88), whose species occur both in fresh and salt water. A considerable number are believed to be naked (cf. however (99), (166)) with a smooth, striated or ribbed periplast, in many cases allowing of considerable change of shape. According to Kofoid and Swezy ((88) p. 41) such change of shape occurs especially in the antapical region where waste matter is extruded and in the neighbourhood of the longitudinal furrow, where they believe that food is ingested. Some of the freshwater species have, however, been shown (166) to have a delicate cellulose membrane exhibiting a number of equal hexagonal fields (fig. 225 I). The transverse furrow runs approximately across the middle of the cell and is either completely circular, as in the freshwater forms, or slightly spiral, the spiral descending to the left as seen from the dorsal surface (fig. 225 F). Many of the marine species lack chromatophores. In some of them the peripheral cytoplasm contains radially arranged rod-shaped mucilage-bodies which rapidly swell in water to form a wide mucilage-envelope (167).

In *Amphidinium* (22, 39, 88) the transverse furrow is shifted close to the anterior end (fig. 225 H, K), so that the epivalve (*e*) is very small, while in Conrad's *Massartia* (22) just the opposite obtains, the hypovalve being very minute. In *Cochlodinium* (fig. 226 E) the body is spirally twisted with the consequence that the transverse furrow runs more than once (up to four times in *C. augustum*) around the cell, while the longitudinal furrow is more or less curved. *Gyrodinium* (cf. p. 680 and fig. 225 E), which also belongs to the Gymnodiniaceae, shows only a slight spiral twist. These forms, as far as our present knowledge goes, are all naked.

A very remarkable organism, often placed in a separate family, is the marine *Polykrikos* (10, 74, 136, 138), one of the few motile colonial types so far known among Dinophyceae (cf. also *Gonyaulax series*, p. 697). In *Polykrikos* (fig. 226 A) two, four, or eight *Gymnodinium*-like individuals are united to form a chain, in which all the cells are orientated in the same sense, the longitudinal furrows being combined to form a common sulcus (*s*) which extends nearly to the two ends of the chain. Each individual possesses both transverse (*t*) and longitudinal (*l*) flagella. It is remarkable that the number of nuclei (*n*) is often less than the number of component individuals, the proportion being usually 1 : 2. The pairs of flagella of two individuals are connected by rhizoplasts to a single nucleus (19*a*). Chromatophores appear to be absent and nutrition is holozoic, as in many of the non-holophytic

Gymnodiniaceae. According to Lebour (95) the sand-inhabiting form of this genus (p. 665) shows lateral compression, possesses chromatophores and lacks the nematocysts found in the ordinary form.

These nematocysts are complex structures typically found in Coelenterata, but among the Dinophyceae only represented in *Polykrikos* and in *Nematodinium* (fig. 226 G, *m*), a member of another family of

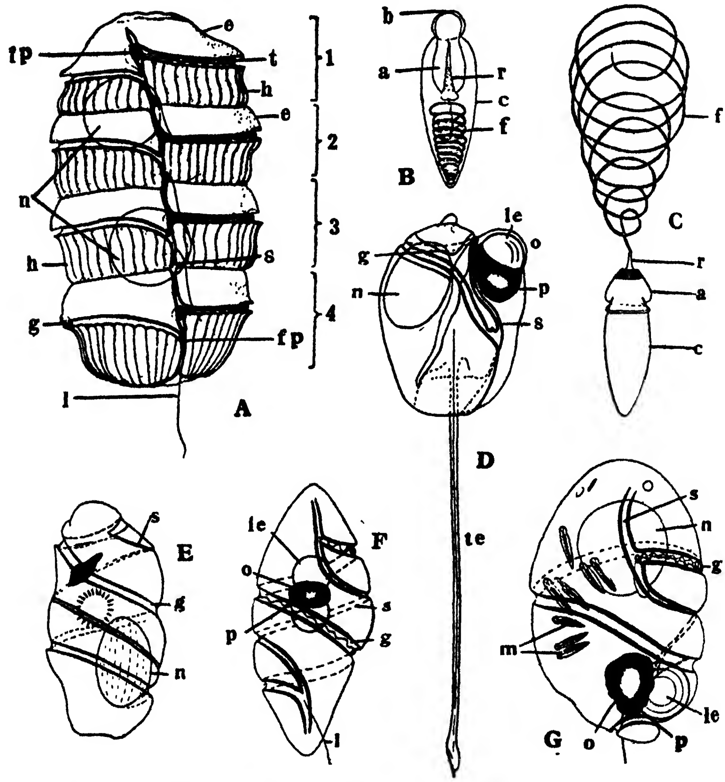

Fig. 226. Dinoflagellata. A–C, *Polykrikos Kofoidi* Chatton; A, colony of four individuals; B, nematocyst; C, the same after discharge. D, *Erythropsis cornuta* (Schütt) Kof. et Swezy. E, *Cochlodinium archimedes* (Pouchet) Lemm. F, *Warnowia fusus* (Schütt) Lindem. G, *Nematodinium armatum* Dogiel. *a*, ampulla (introvert); *b*, cap of nematocyst; *c*, capsule of same; *e*, epivalve; *f*, thread of nematocyst; *fp*, flagellar pore; *g*, girdle; *h*, hypovalve; *l*, longitudinal flagellum; *le*, lens of ocellus; *m*, nematocyst; *n*, nucleus; *o*, ocellus; *p*, pigment-body of same; *r*, axial part of nematocyst bearing the thread; *s*, sulcus; *t*, transverse flagellum; *te*, tentacle. (A after Kofoid; E after Pouchet; F after Schütt; the rest after Kofoid & Swezy.)

Gymnodinioideae (cf. below). Broadly speaking such a nematocyst consists of an oval capsule (fig. 226 B, C, *c*) covered by a rounded cap (*b*) and containing an inverted sack-like extension (the introvert or ampulla, *a*). This includes a special axial structure (*r*) which bears a slender spirally coiled thread (*f*). When the nematocyst is discharged, the inverted sack is protruded and bears the now loosened spiral thread at its apex (fig. 226 C).[1] The exact function of these structures in these forms is unknown. Kofoid and Swezy ((88) p. 60) also record trichocysts in *Polykrikos*, as well as in *Gymnodinium* and *Gyrodinium*.

Nematodinium (88, 102) (fig. 226 G), together with *Warnowia* (*Pouchetia* Schütt[2] (152)) (fig. 226 F), *Erythropsis*, and other genera, belongs to the family Warnowiaceae, whose chief difference from the Gymnodiniaceae lies in the possession of *ocelli*, found only in this family of Dinokontae. The ocelli are highly specialised structures (cf. (88), (152)), probably serving for light-perception, and are composed of a refractive, colourless, often spherical, lens (fig. 226 D, G, *le*) (sometimes consisting of a number of units) and a mass of pigment (*melanosome*, *p*) within which the lens is partly buried. The pigmented cytoplasm is able to move freely around the lens, sometimes completely obscuring it, at other times surrounding only the basal part; sometimes long branches are protruded from it into the surrounding cytoplasm. In the more specialised forms the centre of the melanosome is occupied by a core of highly coloured pigment commonly red, which is apparently connected with the lens and around which the remaining black amoeboid part of the melanosome is distributed. The ocelli are usually found in the posterior part of the body, to the left of the longitudinal furrow and between the two extremities of the transverse furrow (fig. 226 G), the lens being placed anterior to the pigment-mass. There is considerable variety in the differentiation of this structure within the Warnowiaceae (see (88) p. 24 et seq.).

Opinions differ whether the ocellus of these forms has any direct connection with the eye-spot found in many freshwater Gymnodiniaceae, but absent from the marine forms. Such eye-spots appear to be mere masses of granular pigment, situated near the point of origin of the longitudinal flagellum (fig. 225 A, *o*). The researches of Mast on the eye-spot of the Volvocales (p. 33), however, disclose a fundamental similarity with the structure of the ocelli just discussed and it is probable that the latter are merely elaborate developments of the ordinary eye-spot (cf. also (152)). Kofoid and Swezy (88) suggest that the melanosome of Warnowiaceae may have been formed from the scattered pigment present in the cells of many of these forms, a view for which there is no evidence.

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[1] For a detailed description, see (18), (88) p. 30 et seq.

[2] The name *Pouchetia* had already, previous to Schütt's establishment of the genus, been used for a member of the Rubiaceae.

All the members of the Warnowiaceae appear to lack chromatophores, although the protoplast itself is commonly brightly coloured. In *Nematodinium* (fig. 226 G) and *Warnowia* (fig. 226 F) the body is twisted and the markedly spiral transverse furrow makes more than one complete turn about the body, while the longitudinal furrow is similarly twisted (cf. *Cochlodinium*). In *Erythropsis* (43, 58, 87, 123) (fig. 226 D), with a very large ocellus whose lens (*le*) shows asymmetric lamellation, a long process (*tentacle*, *te*) arises from the posterior end of the longitudinal furrow, reaching twice the length of the body in *E. cornuta*. This tentacle, which appears to be a special differentiation of the margin of the sulcus (cf. *Noctiluca*, p. 691), exhibits rhythmic contractions and possesses a complex structure with an axial group of contractile fibrils and a series of circular ones (43). Busch (13) suggests that its main purpose is to maintain the organism in a vertical position in the water. The longitudinal flagellum is often absent, but is sometimes present alongside of the tentacle. In *Proterythropsis* (88, 109) the tentacle is quite short, while the transverse furrow which lies near the apex in *Erythropsis*, is located in the middle of the body.

THE PARASITIC GYMNODINIOIDEAE (BLASTODINIACEAE)

Only brief mention can be made of the interesting series of marine parasitic forms, classed as Blastodiniaceae, for our knowledge of which we are largely indebted to Chatton's investigations ((17), (19); cf. also (102) p. 54). Some are ectoparasites (*Oodinium*, *Apodinium*, etc.), others endoparasites (*Blastodinium*, *Schizodinium*); most of them attack various Metazoa (Crustacea, Pteropoda, Annelidae, etc.), but *Paulsenella* is an ectoparasite on the diatom *Chaetoceras*. Their relationship to other Gymnodinioideae is shown not only by the structure of their small swarmers which possess the usual furrows with transverse and longitudinal flagella (fig. 227 C, J), but also by the cytological features (large nucleus, etc.). Several were first described as species of *Gymnodinium* (cf. (29)).

In the case of *Oodinium* (11, 17) the parasitic stage of *O. Poucheti* found on the Tunicate *Oikopleura dioica* Fol., appears as a spherical or ovoid structure surrounded by a delicate cuticle and attached by a basal cushion (cf. fig. 227 A, *a*). When mature these structures become detached and are found floating freely in the water, where they divide successively to form numerous *Gymnodinium*-like swarmers (fig. 227 C) whose further fate after liberation is not known. In *Apodinium* (15) the ectoparasite is attached by a slender stalk of complex structure (fig. 227 B, D) and the process of swarmer-formation (fig. 227 D, E) is complicated by the fact that the lower (trophocyte, *tr*) of the two individuals formed at each division secretes a new envelope and delays its further division until the upper (sporocyte, *g*) is dividing for the second time. The successive ruptured

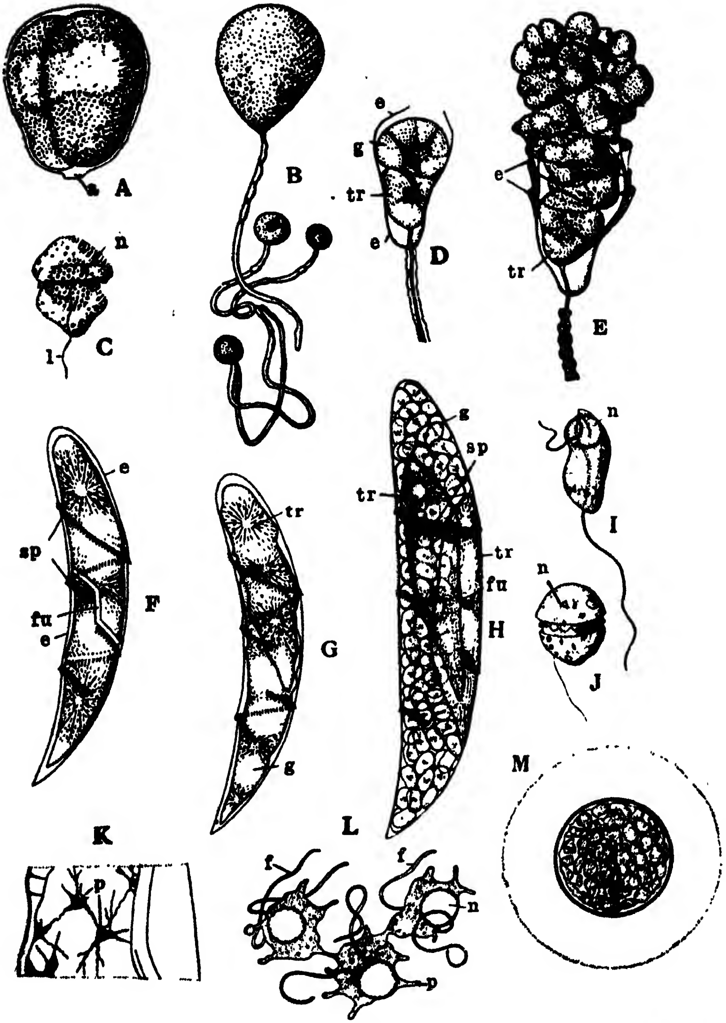

Fig. 227. Blastodiniaceae. A, C, *Oodinium Poucheti* (Lemm.) Chatt.; A, detached parasitic stage, dividing; C, swarmer. B, D, E, *Apodinium mycetoides* Chatt.; B, four individuals attached at the same point, the lowest with two attaching threads; D, the first division; E, later stage of multiplication. F–H, J, *Blastodinium spinulosum* Chatt.; F, cyst; G, first division; H, late stage of division with two trophocytes (*tr*) and 64 sporocytes (*g*); J, swarmer. I, K–M, *Paradinium Poucheti* Chatt.; I, swarmer; K, plasmodial stage; L, amoeboid swarmers liberated from spherical reproductive cells (M). *a*, attaching cushion; *e*, envelope; *f*, flagellum; *fu*, furrow; *g*, sporocyte; *l*, longitudinal flagellum; *n*, nucleus; *p*, pseudopodium; *sp*, spines of envelope; *tr*, trophocyte. (All after Chatton.)

envelopes (*e*) formed by the lower individuals fit into one another as a series of open cups (fig. 227 E).

Blastodinium (14) occurs usually as loose sack- or sickle-shaped cysts within the intestines of marine pelagic Copepods. In *B. spinulosum* Chatt. (fig. 227 F) one end of the cyst is pointed, while the other is rounded; the coarse transparent envelope (*e*) bears two spirals of short spines (*sp*), which commence near the ends and terminate a short distance before the middle of the cyst. Beneath these lines of spines the protoplast is furrowed (*fu*), the two furrows being connected in the equator of the cyst. As in *Apodinium*, one of the two individuals formed by the first division of the protoplast (fig. 227 G, *tr*) remains quiescent, while the other (*g*) divides repeatedly to form numerous (250–500) sporocytes (fig. 227 H, *g*); ultimately the envelope ruptures and the sporocytes escape into the water through the abdominal aperture of the Copepod. They divide once again to give rise to gymnodinioid swarmers which are stated to possess chromatophores (fig. 227 J). The quiescent individual (trophocyte) formed by the first division secretes a new envelope and, after dividing, the one half again proceeds to form a series of sporocytes. It is not known how often this may be continued. A peculiar feature of all these parasitic forms is that nuclear division takes place well in advance of the division of the protoplast, so that all the stages are binucleate until the final division which provides the uninucleate swarmers. Hovasse (63) has found *Blastodinium* in Medusae and other animal hosts, but suggests that its presence there is due to the latter feeding on the primary hosts (the Copepods).

In some of the endoparasites (e.g. *Paradinium* found in the coelome of the Copepod *Acartia Clausi* Giesbr. (16)) the parasitic stage takes the form of naked amoeboid, plasmodial structures (fig. 227 K) with long thread-like pseudopodia (*p*). Fragments of the plasmodia are extruded from the host as spherical structures surrounded by a firm membrane and provided with a wide mucilage-envelope (fig. 227 M). Within these cells amoebae (fig. 227 L) provided with two flagella (*f*) are produced in considerable numbers; they remain united by their short blunt pseudopodia (*p*) for some time after liberation, but ultimately separate and round off to form the swarmers (fig. 227 I).

THE AFFINITIES OF THE GYMNODINIOIDEAE

The Warnowiaceae and Blastodiniaceae clearly represent specialised developments of the type seen in the Gymnodiniaceae which, especially in such forms as *Gymnodinium*, constitute the simplest known members of the true Dinokontae. The relation of the Gymnodiniaceae to the simpler Desmokontae remains rather problematical. Most recent authorities (88, 102, 145) place at the base of the Gymnodinioideae the marine, colourless genera *Pronoctiluca*,[1] *Oxyrrhis*, and *Entomosigma* which are grouped in the family Pronoctilucaceae. These genera are naked or provided with a membrane, possess ill-developed furrows and the flagella are placed ventrally, either near the anterior (*Entomosigma*, fig. 228 A; *Pronoctiluca*,[2] fig. 228 C) or posterior (*Oxyrrhis*, fig. 228 E) end.

Entomosigma (143–145), of which at present a solitary species is known from the Mediterranean (fig. 228 A), has cells running to a point at the anterior extremity, the faintly S-shaped longitudinal furrow (*s*) separating the protoplast into two unequal portions. The transverse furrow is very short and extends round the lip-like prominence at the anterior end (fig. 228 B, *g*). The two flagella arise within the longitudinal furrow, the shorter lying within the latter and being directed anteriorly (fig. 228 A, *l*), while the longer (*t*) is transversely orientated and performs loop-like movements about the front end. The posterior extremity is occupied by a prominent food-body (*fb*). The membrane is rather coarse.

In *Pronoctiluca* (42, 128, 145) (fig. 228 C, K) the transverse furrow is again small, indistinct, and anterior[2] in position, passing for only about one-quarter of the circumference around the cell, while the longitudinal furrow (*s*) extends from it as a deep trough towards the anterior end. From the dorsal margin of this furrow arises a blunt rod-like tentacle (*o*), which is directed anteriorly[2] and is often markedly flexible and mobile. In one of the species the longitudinal flagellum is reduced to a short lash, and it is not improbable that the tentacle plays a considerable rôle in forward propulsion. The membrane is usually punctate (shown only on the left in fig. 228 C), while a large mass of a substance like starch (*a*) is located posteriorly.

In *Oxyrrhis* (51, 155) the transverse furrow (*g*) is situated towards the posterior end and extends from the point of origin of the flagella around the dorsal surface, but loses itself on the right-hand side of the individual (as seen from the dorsal surface) (fig. 228 E, F); its anterior margin is developed as an overhanging lip (fig. 228 F′). The longitudinal furrow is a broad structure which occupies a considerable part of the posterior region of the ventral surface and is divided into two by a pear-shaped lobe (tentacle?) (fig. 228 E, F, *o*), arising from the anterior lip of the transverse furrow and separating the two flagellar pores.

It cannot be denied that there are considerable similarities between *Entomosigma* and *Pronoctiluca* (if the orientation assumed above is

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[1] This is the *Protodinifer* of Kofoid and Swezy (88) and the *Pelagorhynchus* of Pavillard (125).

[2] The orientation of the individuals in this genus is not yet certainly established and it is possible that the tentacle and transverse furrows are really posterior, with the flagella inserted near that end.

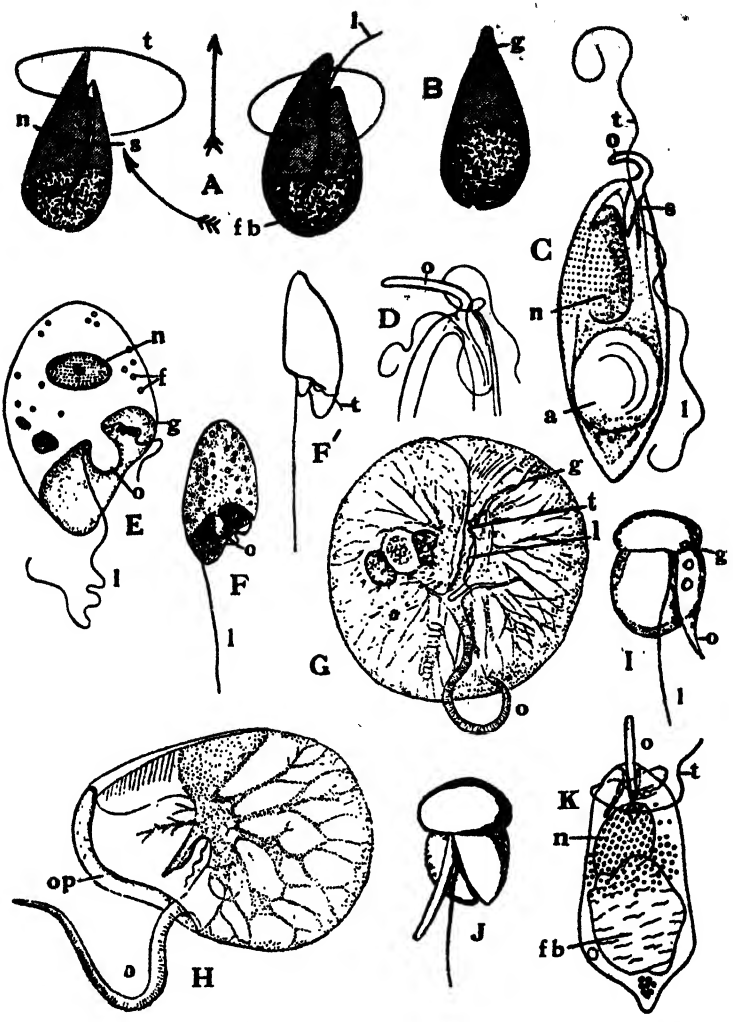

Fig. 228. A, B, *Entomosigma peridinioides* Schill.; A, from the ventral and B, from the dorsal surface. C, D, *Pronoctiluca pelagica* Fabre-Domergue; in C the surface-marking is shown on the left; D, the apex enlarged. E, F, F′, *Oxyrrhis marina* Duj.; F′, side-view. G–J, *Noctiluca scintillans* (Macart.) Kof. et Swezy; G, postero-ventral view; H, view from left side; I, J, swarmers. K, *Pronoctiluca tentaculatum* (Kof. et Swezy) Fabre-Domergue. *a*, food-reserve (starch?); *f*, fat; *fb*, food body; *g*, girdle; *l*, longitudinal flagellum; *n*, nucleus; *o*, tentacle; *op*, cytostome (in H); *s*, sulcus; *t*, transverse flagellum. (A, B after Schiller; C, D after Pavillard; E after Hall; F after Senn; F′ after Lebour; G after Robin; H after Allman; I, J after Cienkowski; K after Kofoid & Swezy; G and H slightly modified, after the same.)

correct) on the one hand, and *Haplodinium* (p. 672) among the Desmomonadaceae on the other. *Oxyrrhis* is supposed to illustrate a further shifting of the flagella and furrow-system on to the ventral surface, combined with an altered orientation of the longitudinal flagellum, and thus to lead over to the main series of the Gymnodinioideae (cf. (88) p. 89). The members of the Pronoctilucaceae, however, give far more the impression of being specialised forms and are hardly suitable as starting-points for the Gymnodiniaceae, which must no doubt be regarded as having been primarily holophytic. The three genera, moreover, scarcely constitute a clearly allied group and one may feel some doubts about their being referred to the same family.

Among the Cryptophyceae the case for a ventral shifting of the flagella and furrow is clear (cf. p. 657) and possibly *Entomosigma* illustrates the same in relation to the Desmomonadaceae. That such a shifting must have occurred also in the evolution of the Gymnodinioideae is patent, but when it took place and exactly from what type of ancestry is by no means so evident. The varied position of the flagellar apertures and the furrow-system on the ventral surface among Gymnodinioideae shows that shifting has often taken place during evolution within the family. It must be confessed, therefore, that the origin of the Gymnodiniaceae, which are best regarded as the most primitive members of the Dinokontae, is at present quite unclear. It may be taken for granted, however, that they originated from holophytic forms and that all the special developments among Gymnodinioideae that cause them to lean so heavily towards the animal side are later acquisitions.

THE CYSTOFLAGELLATA

Many authorities ((5a) p. 331, (49), (70) p. 203, (84), (102) p. 47, (119) p. 50) now regard the Cystoflagellata, and particularly *Noctiluca*[1] (fig. 228 G, H), as a special offshoot of the Gymnodinioideae (cf. however (140)). The subreniform or spheroidal protoplast of the mature individual is here inflated by numerous large vacuoles which probably constitute the means by which the cells float. The longitudinal flagellum (fig. 228 G, *l*) is small but recognisable, while the transverse one (*t*) is represented only by a tooth. The transverse furrow (*g*) is strongly reduced, while the sulcus is elaborately developed and includes a cytostome (fig. 228 H, *op*). There is a prominent tentacle (fig. 228 G, *o*) which is presumably homologous with that of *Erythropsis* (p. 686). Peters (131) records the occurrence of green symbionts in the neighbourhood of the cytostome. No detailed description of this elaborate form is possible

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[1] Very similar is the medusa-like *Leptodiscus* (57).

here, and the reader is referred to the account of Kofoid (84) and the other relevant literature (1, 21, 70a, 137, 139).

Reproduction is accomplished by division, prior to which the structure undergoes simplification. At times multiple fission leads to the formation of numerous small swarmers (fig. 228 I, J) possessing a transverse furrow (*g*), a well-developed longitudinal flagellum (*l*), a small tentacle (*o*), and a marked general resemblance to one of the Gymnodiniaceae; these swarmers, however, possess no transverse flagellum (21). According to van Goor (49) and various earlier workers (see (140)) conjugation of two equal individuals also occurs, the zygote lacking a tentacle and passing through a resting period at the end of which swarmer-formation takes place; it is suggested that reduction occurs during the first division leading to swarmer-formation. Actual copulation has, however, not been observed and it remains doubtful whether the described phenomena do not merely represent stages in division. Hofker (61) believes he has established a conjugation between the swarmers in *N. scintillans*.

(*b*) THE ARMOURED DINOFLAGELLATA

The Amphilothaloideae (88, 102, 152, 172) comprise a few Dinoflagellata which are exceptional in possessing an elaborate internal skeleton which is sometimes silicified. They exhibit certain features which relate them to Radiolaria, as well as to the Ebriaceae (p. 558) (174–176). In the majority of the advanced Dinoflagellata the cell is provided with a firm envelope or armour, usually composed of a series of separate plates grouped in a characteristic manner. In the little known freshwater *Kolkwitziella* (97, 98), however, the brown- or grey-coloured envelope apparently consists of a single piece (fig. 229 A). The transverse furrow is well marked and the longitudinal one extends almost to the antapical pole. Chromatophores are probably present.

THE PERIDINIOIDEAE

In the Peridinioideae, the main series of the armoured Dinoflagellata, the majority of the species possess chromatophores and are essentially holophytic. As in the Dinophysiales and the Gymnodinioideae we can distinguish an apical *epivalve*, an antapical *hypovalve*, and the intervening *girdle* (fig. 229). Each of these is made up of a series of *unequal* polygonal plates, the number and arrangement of which is an important aid in classification, although Lindemann ((97), (99), (100), cf. also (96)) has shown that there is considerable variation among the individuals of a population. Adjacent plates of the envelope usually overlap by their knife-like margins (fig. 230 C, F) which are firmly cemented together, the sutures between them being often but

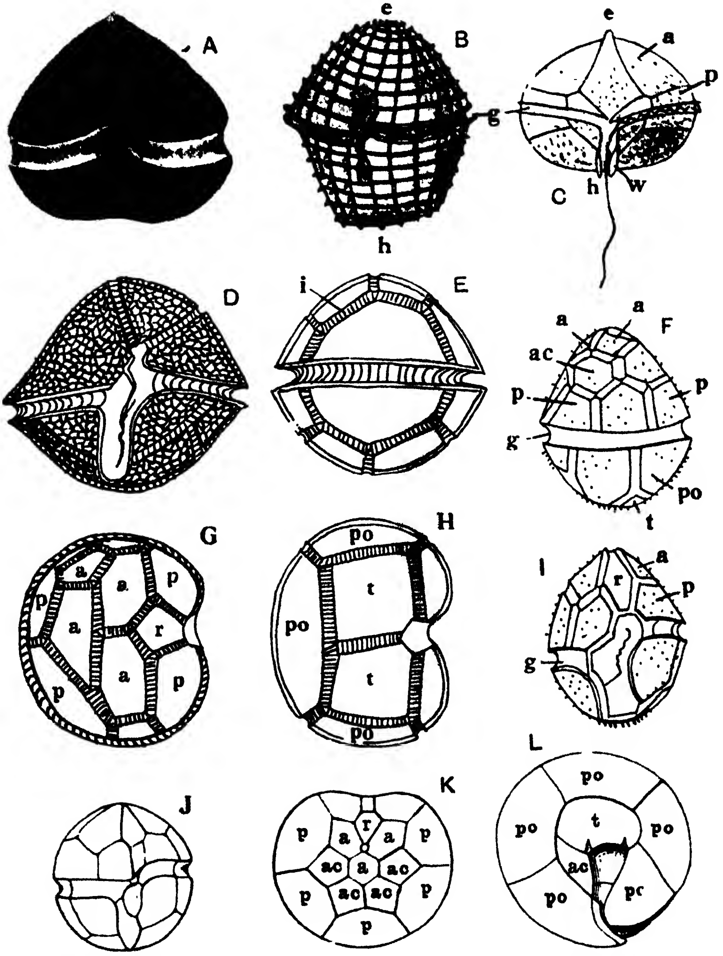

Fig. 229. A, *Kolkwitziella salebrosa* Lindem. B, *Protoceratium reticulatum* (Cl. et L.) Bütschli. C, *Diplopsalis lenticula* Bergh. D, E, G, H, *Peridinium cinctum* Ehrenb. var. *Lemmermanni* West; D, ventral and E, dorsal views; G, epivalve; H, hypovalve. F, I, *P. anglicum* West, dorsal and ventral views respectively. J, K, *Glenodinium cinctum* Ehrenb., from the ventral side and from the apical pole respectively. L, *Gonyaulax spinifera* (Cl. et L.) Dies., antapical pole. *a*, apical plates; *ac*, accessory plates; *e*, epivalve; *g*, girdle; *h*, hypovalve; *i*, intercalary bands; *p*, precingular plates; *po*, postcingular plates; *r*, rhomboidal plate; *t*, antapical plates; *w*, wing. (A, J, K after Lindemann; B, C after Schütt; I, after Kofoid; the rest after G. S. West.)

not always clearly recognisable (fig. 229 C, J); treatment with warm dilute potash generally causes the plates to fall apart.

Frequently the plates are connected by prominent *intercalary bands*, which are commonly striated (figs. 229 G, H; 230 B, *i*) and which appear to widen considerably in older individuals, thus admitting of some increase in the dimensions of the cell (108, 132). In many species the plates are ornamented by numerous areolations (fig. 229 D) and the margins are frequently produced into ridges or beset with teeth or small spines (fig. 229 F, I). In particular the edges of the girdle are often developed as ridges, making the transverse furrow especially conspicuous (figs. 229 D–F; 230 A, B). In *Protoceratium* (fig. 229 B) there is a system of strong reticulate ridges, often bearing spines at the corners and usually altogether obscuring the limits of the plates forming the membrane (6). The plates are usually pierced by pores (fig. 230 G, H, *o*; cf. p. 667), one of which not uncommonly occupies the centre of each areolation, whilst in many cases there is a particularly conspicuous pore at the apex of the epivalve (figs. 229 I; 230 A).

In the common genus *Peridinium* (Peridiniaceae) (5, 78) the individuals are commonly ovoid or subcircular in outline as viewed from the ventral or dorsal surface (fig. 229 D, E), while an end-view is often reniform owing to the slight concavity of the ventral surface (fig. 229 G, H). The antapical end is frequently produced into a pair of small horns. The broad transverse furrow is faintly spiral, descending to the left or to the right; it usually has projecting rims, and is situated slightly but distinctly below the middle of the body so that the hypovalve is smaller than the epivalve (cf. fig. 229 E, F, I). In *Gonyaulax* (fig. 225 D, p. 681) the transverse furrow is markedly spiral. The broad longitudinal furrow of *Peridinium* often extends beyond the transverse one for a variable distance into the apical half of the individual (fig. 229 D, I). In the closely allied genus *Diplopsalis* (6, 94, 157) (fig. 229 C) the left-hand margin of this furrow is produced into a wing (*w*) which may extend over the antapical pole.

The plates of the epivalve are more numerous than those of the hypovalve which are almost invariably seven in number. Among the former one distinguishes those immediately adjacent to the apex as the *apical plates* (fig. 229 F, G, *a*), whilst those adjacent to the girdle are known as the *precingular* (*pre-equatorial*) *plates* (fig. 229 F, G, *p*); of the latter there are nearly always seven, while the number of apical plates varies. In many species of *Peridinium* one finds on the dorsal surface of the epivalve a number of *accessory plates* intervening between the apical and the precingular plates (fig. 229 F, *ac*). The actual apex of the epivalve may be occupied by a single plate (e.g. *P. bipes* Stein), but is more usually covered by several. Occupying the middle of the ventral surface, and extending from the upper end of the longitudinal furrow either to the apex or close up to the apex of the epivalve, is a characteristic *rhomboidal plate* ("Rautenplatte" of the Germans, fig. 229 G, I, *r*); this is one of the apical plates.

The hypovalve similarly consists of two *antapical plates* (fig. 229 F, H, *t*) and five *postcingular* (*postequatorial*) *plates*, adjacent to the girdle (fig. 229 F, H, *po*); the former cover the posterior extremity of

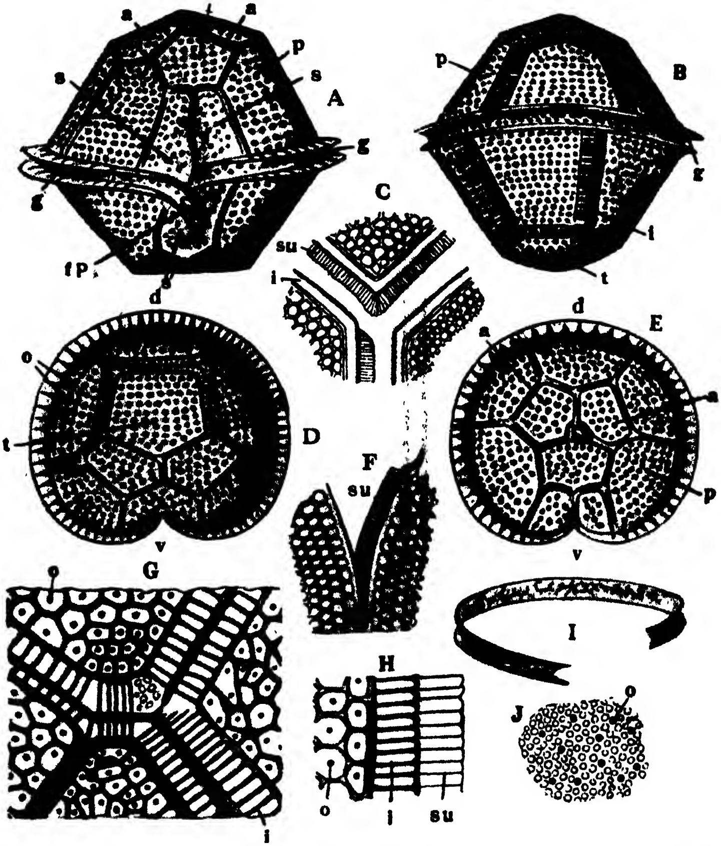

Fig. 230. A, B, D, E, *Goniodoma acuminatum* Stein; A ventral, B dorsal, D antapical, and E, apical views. C, F, *Peridinium ovatum* (Pouch.) Schütt; C, mode of junction of plates; F, two plates partly separated by maceration, showing the connecting edges. G–I, *P. divergens* Ehrenb., var.; G, H, parts of envelope showing pores (*o*) and intercalary bands (*i*); I, the girdle isolated. J, *Dinophysis rotundata* Cl. et Lachm., part of membrane with pores (*o*). *a*, apical plates; *d*, dorsal and *v*, ventral surfaces; *fp*, flagellar pore; *g*, girdle; *i*, intercalary bands; *o*, pores; *p*, precingular plates; *s*, *s'*, plates of sulcus; *su*, suture; *t*, antapical plates. (A, B, D, E after Stein; the rest after Schütt.)

the individual, while the latter are interrupted on the ventral surface by the longitudinal furrow. Mangin (106) has drawn attention to the fact that the suture between the two antapical plates may be curved in contrary directions in different individuals of the same species. There are no accessory plates on the hypovalve of *Peridinium*, but one occurs in *Gonyaulax* (83) (fig. 229 L). In the marine *Goniodoma* (fig. 230 A, B, D, E), which otherwise closely resembles *Peridinium*, there are three antapical plates, two ventral and one dorsal (fig. 230 D, *t*). The girdle and sulcus are no doubt likewise composed of a series of plates, but these are usually not easily recognisable and are at present imperfectly known (cf. (78), (152)); in *Goniodoma*, however, the sulcus consists of two plates above and one below the girdle (fig. 230 A, *s*, *s'*). The girdle often becomes detached as one ring-shaped piece (fig. 230 I).

The simplest members of the Peridinioideae are the Glenodiniaceae with a thin unsculptured envelope which is, however, divided into a series of numerous polygonal, delicately areolate fields, usually only distinguishable with difficulty (100, 166). *Glenodinium* (fig. 229 J, K), except for the inequality of these fields, is very similar to *Gymnodinium*; the majority of its species occur in fresh water and several possess large prominent eye-spots (fig. 220 A, p. 666). The arrangement of the areas on the membrane is very similar to that above described for Peridiniaceae. Conrad (22) has described an allied genus (*Phyllodinium*) which is strongly flattened dorsoventrally. A more specialised form is *Hemidinium* (fig. 225 B, p. 681) in which the markedly spiral transverse furrow occupies only the left half of the elongate-ovoid individual (157, 168).

It can hardly be doubted that the Glenodiniaceae are derived from simple Gymnodiniaceae in which the membrane has undergone differentiation in the direction characteristic of the Peridiniaceae. Young individuals of *Peridinium*, etc., likewise show a simple primary membrane divided into polygonal fields foreshadowing the future plates (*prevalvate stage*, cf. (100), (102), (103) p. 98). According to Schütt ((154) p. 611) this primary membrane is pierced by pores which persist as the centrifugal thickening leading to the production of plates takes place. Similar pores have been recorded in *Hemidinium* (168). The plates of *Peridinium*, etc., are thus superadded on a primary Glenodiniaceous structure (cf. also (105)). According to Kofoid (78) the thick cellulose envelope is bounded externally by a "cuticle".

Of the more specialised members of the Peridinioideae the most widely distributed is the genus *Ceratium* (37, 69, 92, 161), whose species are abundant both in freshwater and marine plankton. They appear to be invariably holophytic. The individuals are markedly asymmetric (fig. 231) and usually strongly flattened dorsiventrally (fig. 231 H). They are produced into one apical and two or three long antapical, hollow horns (fig. 231 A, D) occupied by cytoplasm, the former usually bearing an apical aperture (lacking in *C. hirundinella*). In many of the marine species the antapical horns are curved forwards (fig. 231 E), while the species found in tropical waters in general have longer horns than those from arctic seas (151). The girdle (*g*) is nearly horizontal in its course and divides the body into two approximately equal, but dissimilar halves. The plates composing the membrane are markedly areolated, being connected by rather narrow sutures. On the middle of the ventral surface there is a large rhombic, unsculptured, hyaline area (*h*) which interrupts the transverse furrow. Kofoid ((78) p. 29) regards the whole of the hyaline area as homologous with the longitudinal furrow of a *Peridinium*, but on other interpretations the longitudinal furrow occupies only the left-hand margin of this area. The opposite margin often harbours a funnel-shaped groove (absent in *C. hirundinella*) which serves to accommodate the apical horn of the next individual when temporary colonies are formed (fig. 231 E).

Such colonies occur in marine species (8, 107), but often consist of only two individuals. Colony-formation is also known in *Gonyaulax* and in *G. series* (85) the successive individuals are separated by but slight constrictions and there is a progressive reduction in size in passing from the central to the terminal individuals. Owing to the practically complete fusion of the individuals their apical and antapical regions are non-developed, but the entire envelope is found in initial stages of formation on the terminal individuals. The cell-contents form an unbroken axial mass of cytoplasm, but it is probable that there is a nucleus to each individual (cf. also (82)). This case should be compared with *Polykrikos* (p. 683).

There are in *Ceratium* four apical plates[1] (fig. 231 H, *a*), a number of which combine to form the apical horn (fig. 231 I), and two antapical plates producing one of the antapical horns, while the others arise from postcingular plates (fig. 231 I, *po*) which like the precingular ones are five in number (fig. 231 H); there are no accessory plates.

In the abundant freshwater species *Ceratium hirundinella* (fig. 231 A) the antapical horns are two or three in number and, both in this respect as well as in the relative lengths of the different horns and their size as compared with the main body of the cell, there is a great deal of variability.[2] Amman (2) records specimens found in spring with a single antapical horn. Continental observations on the occurrence of this ubiquitous species have frequently demonstrated a certain periodicity in the appearance of three- and four-horned forms and in the size of the body (cf. especially (28)). According to Krause (90) the length of the apical horn is equal to the difference in length between the two main antapical horns multiplied by the number of

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[1] Very rarely three or five (154*a*).

[2] Cf. (23), (40), (50), (66), (90), (92), (104), (162), (163).

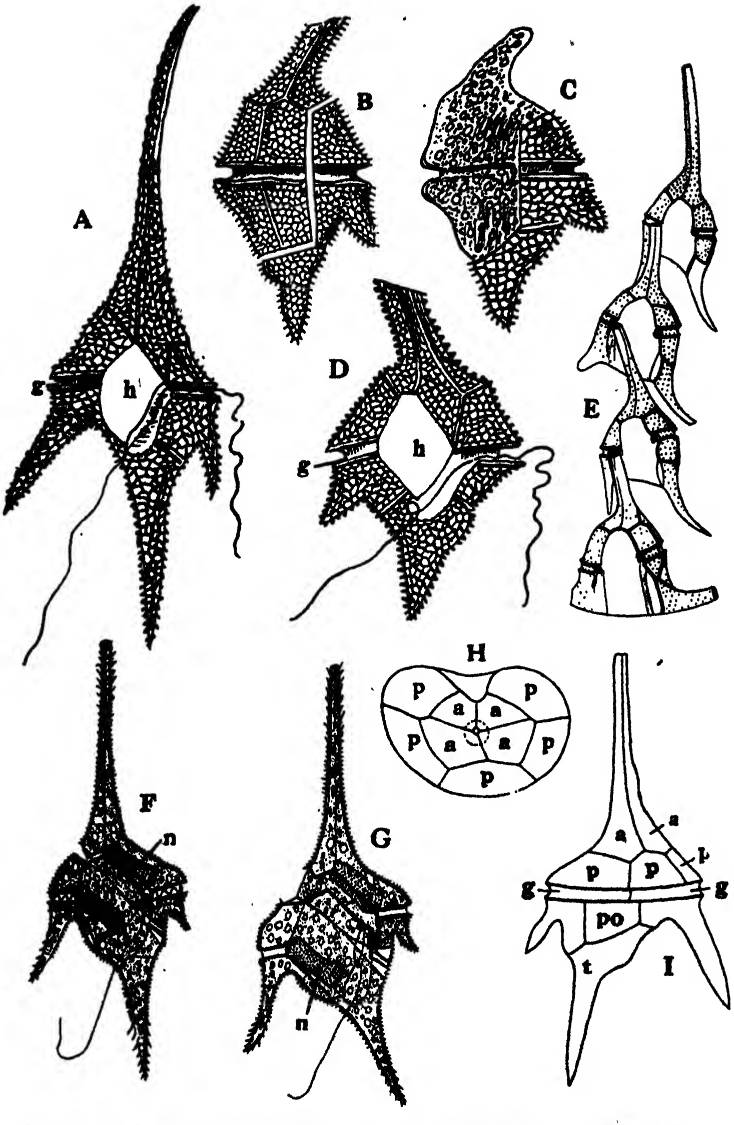

Fig. 231. The genus *Ceratium*. A, F–I, *C. hirundinella* O. F. M.; A, four-horned individual from the ventral surface; F, G, successive stages in division; H, arrangement of plates on epivalve; I, the same in a dorsal view of an

horns. He is of the opinion that the various forms often found intermingled in the same piece of water represent stages in the development of the normal form. Pearsall (130) relates the decrease in size observed from summer onwards to alterations in the character of the wall. Entz (173) has studied the relation between surface and volume during the growth of this species.

Many of the marine species at times shed the greater part of their horns by the formation of circular clefts due to local solution of the cellulose wall. This of course leads to a reduction in specific surface which will result in sinking, and such individuals with stunted horns are indeed most abundant in collections from deeper levels (76). Kofoid suggests that this phenomenon is related to temperature-changes. The same authority (81) has drawn attention to the fact that the frequent asymmetry evident in the processes of *Ceratium* and other Dinoflagellata has the effect of causing the organism to assume a position with the long axis horizontal as soon as it commences to sink. This will appreciably decrease the rate of drop, while not interfering with progression by means of the flagella, since it is combined with rotation of the organism around its long axis. In a number of the species of *Ceratium* sudden changes after division on the part of one or more individuals and apparently of the nature of mutations have been recorded (77).

Apart from the genera already considered there is considerable diversity in the organisation of the Peridinioideae. In *Ceratocorys* (80, 157) (fig. 232 A) the transverse furrow (*g*) is shifted close to the apical pole and its margins are commonly markedly produced as prominent collars below the relatively small lid-shaped epivalve (*e*). There is thus a certain superficial similarity with *Phalacroma* (p. 675). The hypovalve (*h*) usually possesses a number of long processes with a definite central axis. In Kofoid's *Acanthodinium* ((75) p. 193) almost every plate of the envelope is provided with a long process, forked at its extremity (fig. 232 B). The pear-shaped individuals of *Podolampas* (79, 157) (fig. 232 C) are peculiar in lacking a marked transverse furrow, its place being taken by a narrow band-shaped strip (*g*) which is scarcely sunk and is fused to the lower ends of the precingular plates.

individual. B–D, *C. cornutum* Clap. et Lachm.; B, early stage in division; C, one of the daughter-individuals before the new half of the membrane is formed; D, fully grown individual, ventral surface. E, *C. tripos* (O. F. M.) Nitzsch, colony. *a*, apical plates; *g*, girdle; *h*, rhombic area; *n*, nucleus; *p*, precingular plates; *po*, postcingular plates; *t*, antapical plates. (E after Kofoid; F, G after Lauterborn; H, I after Lindemann; the rest after Schilling.)

(*c*) THE PALMELLOID DINOFLAGELLATA (DINOCAPSINEAE)

Only one palmelloid form has so far been described among Dinokontae, the genus *Gloeodinium* ((73) p. 411, (119) p. 45, (141)).[1] This is a moorland alga with packets of rather large cells embedded in stratified mucilage and showing the typical structure of the Dinophycean cell, except that furrows are not recognisable (fig. 232 D, E). Killian (71) records reproduction by swarmers resembling a *Hemidinium* and Geitler ((48) p. 223) states that he can confirm this. Pascher ((119) p. 46) speaks of other freshwater and marine Dinocapsineae without giving details.

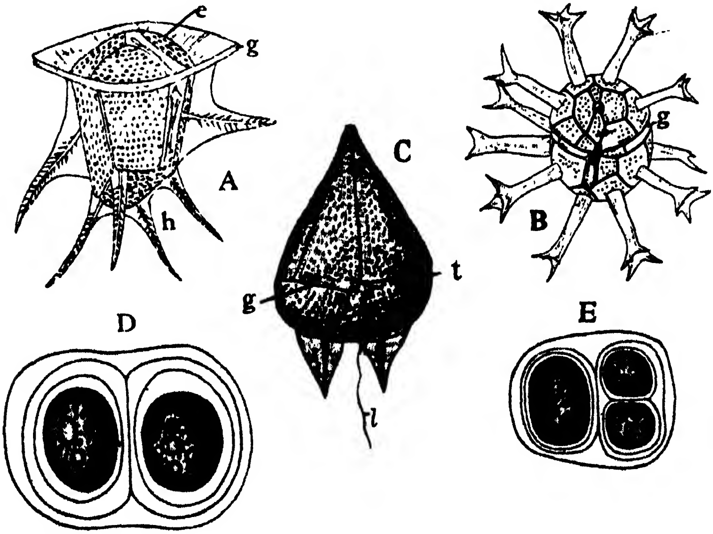

Fig. 232. A, *Ceratocorys horrida* Stein, individual viewed from the right-hand side, showing part of the ventral surface. B, *Acanthodinium caryophyllum* Kof., ventral view. C, *Podolampas bipes* Stein, ventral view. D, E, *Gloeodinium montanum* Klebs. *e*, epivalve; *g*, girdle; *h*, hypovalve; *l*, longitudinal flagellum; *t*, transverse flagellum. (B after Kofoid; D, E after Klebs; the rest after Stein.)

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[1] According to Geitler ((48) p. 223) the alga known as *Chroococcus macrococcus* is identical with *Gloeodinium montanum*.

THE REPRODUCTION OF THE DINOFLAGELLATA

The essential facts relating to the reproduction of *Noctiluca* (p. 692) and of the Blastodiniaceae (p. 686) have already been given and the subsequent matter deals with the remaining forms regarding which our information is rather fragmentary. The ordinary method of multiplication is by division of the cells (31) and this usually takes place obliquely along the longitudinal axis (figs. 233 B, C; 231 B, C, F, G). The process shows various modifications, but several of these can occur at different times in the same species ((88) p. 69, (102), (103)).

In some cases (*Gymnodinium*, *Ceratium*) division occurs during movement, each daughter-individual receiving one flagellum from the parent and forming the other afresh (cf. figs. 231 F, G; 233 A; and 220 G, p. 666). In *Gymnodinium*, *Glenodinium*, and a few species of *Peridinium*, the entire individual often divides, the envelope when present not rupturing, but growing over the surface of the dividing protoplast *pari passu* with its fission (fig. 233 A). In *Ceratium* (37, 107) (also in *Gonyaulax* according to Kofoid (76)), on the other hand, the elaborate envelope splits into two, the line of rupture always running between definite plates (fig. 231 B, C, F, G). As the enlarging protoplast divides, the two portions exposed by the rupture of the parent-envelope gradually assume the characteristic shape of the species (fig. 231 C), but it is not until some little time after fission is complete that the missing plates of the membrane are gradually formed. In *Ceratium cornutum*, according to Mangin (107), the two daughter-cells are orientated at right angles to one another. Multiplication by a kind of budding has also been recorded for *Ceratium* (4, 8) and is stated to be associated with amitotic division of the nucleus (cf. however (52)).

In many cases division is effected during a sedentary phase (71 *a*, 148). Cessation of movement is followed by a more or less marked contraction of the protoplast (fig. 233 B). Oblique division may then either follow at once, the two new individuals being set free by the rupture of the parent's membrane (e.g. *Peridinium*, fig. 233 C, D), or the protoplast divides only after it has escaped from the latter. Frequently the contracted protoplast acquires a new membrane before its liberation from the old one (fig. 233 M) and the thin-walled, commonly spherical cysts thus formed may rest for a varying period. In most cases, given favourable conditions for development, they are merely a passing phase, the protoplast soon dividing (fig. 233 L) to form new motile individuals. At other times the escaped protoplast becomes enveloped in mucilage (152, 160) and may apparently divide several times within the envelope thus provided (fig. 233 E).

The protoplast of the armoured forms appears not infrequently to escape as a naked gymnodinioid swarmer (fig. 233 G, H) which,

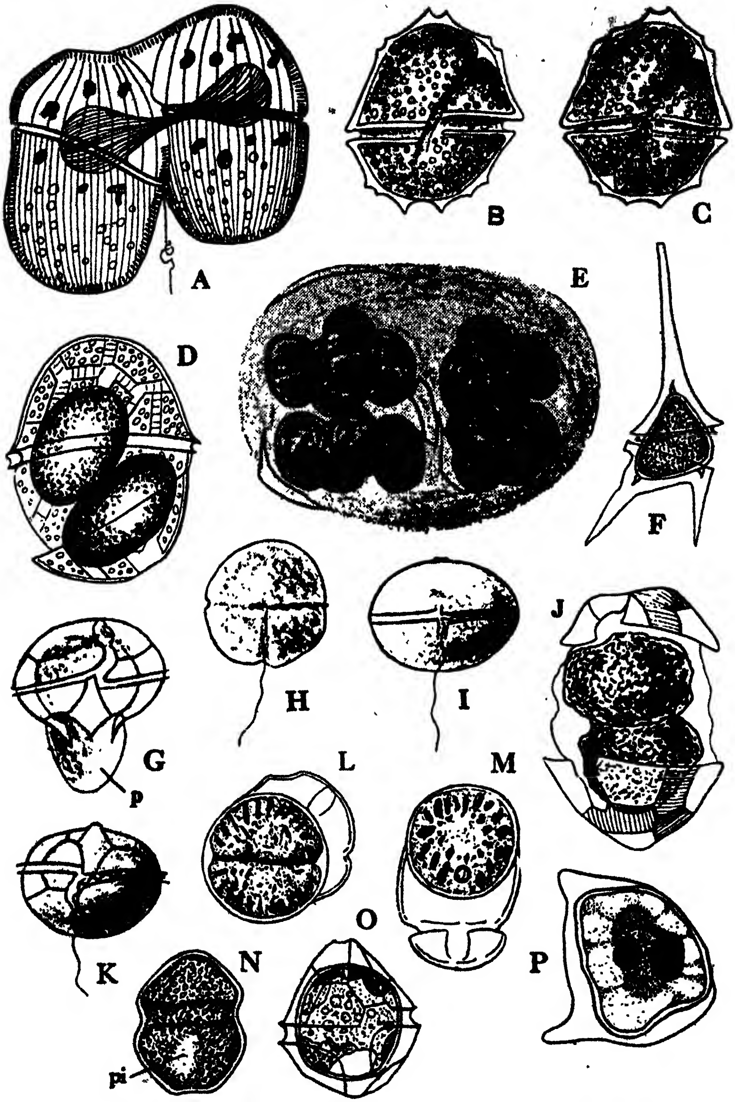

Fig. 233. Reproduction of the Dinoflagellata. A, *Gymnodinium heterostriatum* Kof., dividing individual. B, C, *Peridinium tabulatum* (Ehrenb.) Clap. et Lachm., two stages in division. D, *P.* (*tabulatum*?), completed division. E, Undetermined marine gymnodinioid form showing repeated

without division, after some time secretes a new envelope (76, 121) (fig. 233 I). In such cases of rejuvenescence, as well as in the above-described division-process involving only the protoplast of the armoured forms, the individuals pass successively through a naked (avalvate, fig. 233 G), a gymnodinioid (fig. 233 H), and a prevalvate stage (fig. 233 I, cf. p. 696) before reaching the condition with the mature envelope (fig. 233 K) (cf. especially (36), (103)). This return to the gymnodinioid condition furnishes clear evidence for the view that this represents the primitive type among the Dinoflagellata. Entz (36) also describes for *Peridinium Borgei* stages devoid of flagella but enveloped in mucilage, which exhibit amoeboid movements.

Resting cysts,[1] with a thick membrane and abundant food-reserves and often of characteristic shape, have been observed in a number of species and are certainly of wide occurrence in freshwater forms where they constitute the means of survival during unfavourable periods (164). In *Ceratium hirundinella* they have been shown to retain their vitality for six or seven years (67). They are not always sharply distinguishable from the above-mentioned thin-walled cysts formed prior to division. They are sometimes spherical (fig. 233 O), but commonly possess a distinctive shape (fig. 233 F), occasionally approaching that of the ordinary individual (fig. 233 N). The membrane appears often to consist largely of cellulose, while the contents include glycogen, volutin, and some fat. In *Ceratium* (44, 67) the contents of the germinating cyst escape as a gymnodinioid swarmer, followed soon by the "preceratium" phase in which the typical shape and elaborate system of plates are gradually acquired.[2]

The existence of sexual reproduction[3] among these forms is still a very open question, and there can be no doubt that, if it exists, it is of rare occurrence. Zederbauer (171) and Entz (32, 34) recorded a copulation between the protoplasts of two individuals in *Ceratium*, observations

[1] See (35), (36), (41), (70), (148), (164).

[2] With reference to the influence of external factors on the germination of the cysts and the form of the resulting individuals, see (68).

[3] See also p. 708 (*Hypnodinium*). The sexual reproduction of *Noctiluca* is referred to on p. 692.

division within mucilage, the remnants of the original envelope visible at the periphery. F, P, *Ceratium hirundinella* O. F. M.; F, three-horned individual with cyst; P, binucleate cyst. G–I, K, *Peridinium ovatum* (Pouch.) Schütt., successive stages in rejuvenation; G, escape of protoplast (*p*); H, gymnodinioid stage; I, prevalvate stage; K, mature individual. J, *P. cinctum* Ehrenb., division. L, M, *Glenodinium emarginatum* Klebs; M, escape of cyst; L, division of same. N, *G. Lomnickii* (Wolosz.) Lindem., cyst. O, *Peridinium anglicum* West, cyst within membrane of parent. *pi*, pigment-mass. (A after Dogiel; B, C after Schilling; D, L, M after Klebs; F, O after West; J, N after Lindemann; P after Hall; the rest after Schütt.)

that have been called into doubt by various subsequent writers (68, 70). From more recent observations it appears that such union is due to an escape of cytoplasm from the longitudinal furrow, such protoplasmic exudations uniting with one another in a pair of individuals (cf. (39)). Similar conditions have been observed in marine planktonic forms (122). Many believe the phenomena to be pathological.

Hall (52) describes binucleate cysts in *Ceratium hirundinella* (fig. 233 P) and supposes them to have resulted from sexual fusion. Entz (41) who also observed such cysts, on the other hand, considers them to be due to amitotic division of the nucleus.

(*d*) COLOURLESS AND RHIZOPODIAL FORMS (RHIZODININEAE)

Mention has already been made of the fact that a large number of the Dinoflagellata are colourless, which is especially common in the marine forms. Moreover, in many cases colourless and pigmented species occur in the same genus (*Gymnodinium*). Chodat's *Bernardinium* ((20) p. 40) is a colourless form resembling *Hemidinium* in the fact that the transverse furrow extends only part of the way round the cell (fig. 234 A). Some of the colourless forms are no doubt saprophytes, but a large proportion appear to carry on holozoic nutrition which is readily accomplished owing to the faculty of the protoplast to put forth pseudopodia from the neighbourhood of the flagellar pores (cf. p. 667 and (26), (39), (95), (157)). Certain forms like *Gyrodinium hyalinum* (146) can at such times become perfectly amoeboid (fig. 234 B, C). There is abundant evidence (32, 127), too, that holophytic forms (e.g. species of *Gymnodinium*, *Ceratium*) may occasionally feed in the same way and may then acquire a rhizopodial habit ((60), (89), (116) p. 132, (117)). The Blastodiniaceae are highly specialised parasites, some like *Paradinium* (p. 688) being altogether amoeboid. According to Hovasse and Teissier (64, 65) many of the *Zooxanthellae* of Coelenterata are actually Dinophyceae, a conclusion based on their nuclear characteristics.

In view of these facts it is not surprising that some members of the class have adopted a definite amoeboid form, and one of these, *Dinamoebidium*,[1] has been fully described by Pascher (116). This is a large, colourless, marine amoeba (fig. 234 D) creeping over the substratum with the help of short plump pseudopodia and possessing a large prominent nucleus (*n*) containing numerous fine chromatin threads. No stages of division have been observed, but the organism normally forms elongate cysts, in shape somewhat like the segments of an orange and provided with thickened gelatinous tips (fig. 234 E, F). Within these cysts the protoplast divides successively two or

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[1] First described as *Dinamoeba*.

three times (fig. 234 G, I) and the products (*s*) develop the two furrows characteristic of the Dinoflagellata and escape as gymnodinioid swarmers by complete gelatinisation of one of the apices (fig. 234 H). Particles that had been ingested in the amoeboid stage are left behind

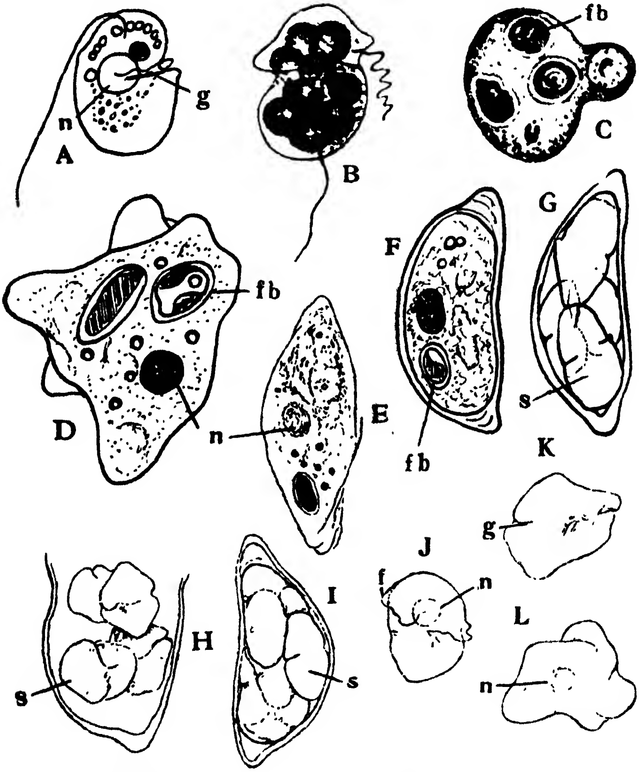

Fig. 234. Colourless and amoeboid Dinophyceae. A, *Bernardinium bernardinense* Chod. B, C, *Gyrodinium hyalinum* (Schill.) Kof. et Swezy; B, flagellate stage; C, amoeboid stage. D–L, *Dinamoebidium varians* Pascher; D, normal (amoeboid) stage; E, the same, shortly before encystment; F, mature cyst; G, I, the same, formation of four and eight swarmers respectively; H, liberation of swarmers; J, swarmer; K, the same, showing metaboly; L, young amoeba. *f*, flagellum; *fb*, food-body; *g*, girdle; *n*, nucleus; *s*, swarmer. (A after Chodat; B, C after Schilling: the rest after Pascher.)

in the empty cyst-membrane. The swarmers (fig. 234 J), which are markedly metabolic, appear to lack the longitudinal flagellum and Pascher comments on the clumsy character of the movements. After a very short motile period the metaboly becomes more and more pronounced and the swarmer gradually changes into an amoeba (fig. 234 K, L), the flagellum apparently being absorbed into the protoplast. The cysts show considerable resemblance to the individuals of the holophytic *Cystodinium* described below.

Dinamoebidium has thus assumed an amoeboid condition in the normal phase of its life, and the flagellate stage is of quite brief duration. Without a knowledge of this phase, however, it would be regarded as one of the Rhizopoda, although its nuclear structure hints at its correct assignation. As already mentioned amoeboid stages are known in species of *Gymnodinium* and *Gyrodinium*, but here they do not appear to represent the normal habit as in the case of *Dinamoebidium*. It is instructive to compare *Dinamoebidium* with similar amoeboid forms among Xanthophyceae (p. 499) and Chrysophyceae (p. 534). Various authorities (cf. (5a) p. 96, (117) p. 75) have commented on the resemblance between the swarmers of some Radiolarians and the naked Dinoflagellata, a matter worthy of further investigation (cf. also p. 692).

Order II. *DINOCOCCALES*

Since Klebs' important memoir (73) on the alga-like Peridinieae, coccoid organisation has been a familiar feature of the Dinophyceae, and our knowledge of these forms has been appreciably extended by Pascher (119). As in other coccoid series, some Dinococcales propagate by zoospores, whilst others exhibit no motile reproductive cells, but the difference in behaviour appears here to be in general only a specific feature.

Cystodinium (47, 73) has more or less lunate cells, with tips often markedly produced, containing numerous parietal brown-coloured chromatophores and a large more or less excentric nucleus (fig. 235 A). In the ordinary vegetative individual there is no indication of furrows or stigma, but these appear in some species as the protoplast contracts prior to division (fig. 235 B, G); at the same time the chromatophores assume a more or less radial arrangement. The contracted protoplast then divides into two or four portions (fig. 235 C, H) which are liberated as swarmers with the typical Dinoflagellate organisation (fig. 235 D); in one species they are naked, whilst in another they are provided with a delicate membrane. In *C. lunare* (119) (fig. 235 E), however, swarmer-formation is altogether suppressed and furrows and eye-spot never appear at any stage of the process of division. The two new individuals are simply liberated as autospores from the ruptured parent-membrane (fig. 235 F). In another species (*C. phaseolus* (120)), with very variable chromatophores, Pascher records the formation of two types of swarmers, the larger directly producing

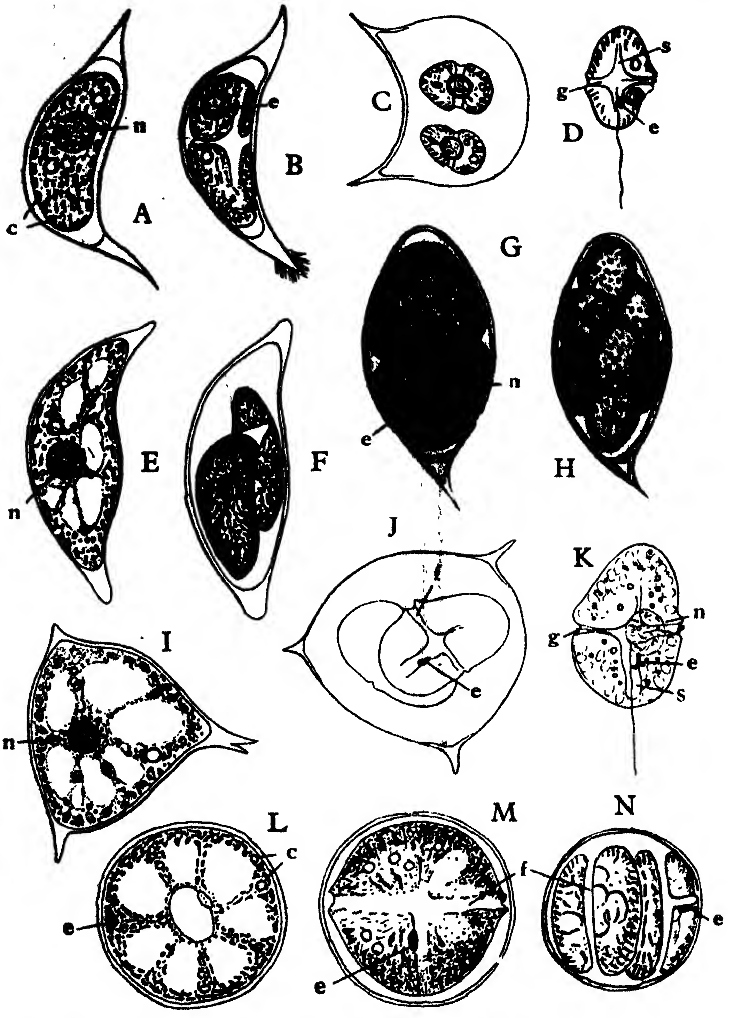

Fig. 235. Dinococcales. A–D, *Cystodinium Steinii* Klebs; A, cell with slightly contracted protoplast; B, incipient division; C, formation of two swarmers; D, swarmer. E, F, *C. lunare* Pascher; E, optical section; F, division-stage. G, H, *C. unicorne* Klebs; G, individual with protoplast showing furrow-structure, etc.; H, division. I–K, *Tetradinium minus* Pascher; I, optical section; J, swarmer-formation; K, swarmer. L–N, *Hypnodinium sphaericum* Klebs; M, incipient division; N, formation of two daughter-cells. *c*, chromatophore; *e*, eye-spot; *f*, furrow; *g*, girdle; *n*, nucleus; *s*, sulcus. (E, F, I–K after Pascher; G, H after Stein; the rest after Klebs.)

new individuals, while the smaller are suspected of being gametes, although fusion has not been observed.

Those forms of *Cystodinium* that reproduce by zoospores are manifestly not very far removed from species of the genus *Gymnodinium*, where the resting cysts represent comparable stages, except that the relative importance of the motile and sedentary phases in their life-cycle is reversed. To the zoologist this may appear to be a difference of little significance (cf. (88) and (102)), but to the botanist familiar with the gradual suppression of motility in other classes of the Protophyta a reference of such forms to the Dinoflagellata would obscure the obvious parallelism. Moreover, a form like *Cystodinium lunare*, which has apparently altogether given up the motile phase, could scarcely be ranked among Dinoflagellata.

In *Tetradinium* (47, 73, 119), a parallel to *Tetraëdron* among the Green Algae but possessing the Dinophycean cell-structure above described for *Cystodinium* (fig. 235 I), reproduction by zoospores appears to be the rule. In this case, however, neither eye-spots nor furrows can be detected in the contracted protoplast prior to division, although both are evident in the pair of gymnodinioid swarmers that are liberated from the ruptured membrane of the parent (fig. 235 J, K). *Dinastridium* (119), with flattened polygonal cells with the angles produced into spines, is so similar that the grounds for a generic separation are not very strong.[1]

A further step in the elimination of the motile phase is seen in *Hypnodinium* (73), with large spherical *Eremosphaera*-like cells (fig. 235 L), whose protoplast often displays a conspicuous eye-spot (*e*). As Klebs showed, division is preceded by a contraction of the protoplast accompanied by furrow-formation (fig. 235 M), the cell-contents at this stage presenting a marked similarity to a *Gymnodinium* devoid of flagella. In this condition the protoplast divides into two (fig. 235 N), but although the products also possess furrows no motile phase ensues. Gradually, as the new individuals round off, the furrows disappear, although the eye-spot may persist for some time; the daughter-individuals acquire new membranes and are sooner or later liberated by rupture of that of the parent. Pascher ((119) p. 34) mentions forms devoid of a stigma and showing furrows only for a brief period. The same authority ((115) p. 152, (119) p. 34, (120) p. 251) has repeatedly referred to the formation in this genus of small, gymnodinioid swarmers,[2] which are stated to be gametes. The resulting zygote is thin-walled and slowly grows until it reaches the size of the ordinary vegetative cell, after which the contents divide to form four swarmers. No further details are at present available,

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[1] Pascher ((119) p. 32) suggests that the colourless marine *Thaurilens* (126), if it be actually an independent form, may belong to this affinity.

[2] Similar swarmers are stated to occur also in other Dinokontae.

but the published facts indicate a course of events that contrasts sharply with the ordinary reproduction of *Hypnodinium*.

Another genus, *Phytodinium* (73, 119) (fig. 236 A, B), resembles *Cystodinium lunare* in the absence of swarmers or of any indication of furrow-formation. The epiphytic *Stylodinium* (73, 119) (fig. 236 C, D) constitutes a parallel to *Characium* among the Chlorococcales and is believed to reproduce by motile stages.

Both Klebs (73) and Pascher (119) include among the Dinococcales the genera *Pyrocystis* (*P. Noctiluca* Murray) and *Dissodinium*.[1] In the latter ((3), (29) p. 4), a marine plankton organism, the normal vegetative condition is represented by a large vesicular cell with a thin membrane and a huge vacuole traversed by delicate protoplasmic strands (fig. 236 E). The large nucleus (*n*) lies towards one side of the cell in a special aggregation of cytoplasm which also contains numerous parietal discoid chromatophores (*c*). Within these individuals there are formed sooner or later by successive division (fig. 236 F, G) as many as sixteen lunate cells resembling the sedentary stage of a *Cystodinium* (fig. 236 J). These structures, after being set free, develop further, as in *Cystodinium*, with the production and liberation of a number (4–8) of gymnodinioid swarmers (fig. 236 K–M) from which the spherical cells presumably again arise. As Pascher points out, we have here the peculiar condition that the organism reproduces first by a kind of autospore-development followed by swarmer-formation on the part of the products.

Pyrocystis (7, 111) is an abundant plankton form in most tropical and subtropical seas and is one of the diverse organisms responsible for phosphorescence. Here the individual throughout life appears as a large spherical cell of a pale yellow colour due to the numerous small yellow-brown chromatophores (fig. 236 H). At the time of multiplication the protoplast contracts greatly (fig. 236 I) and divides into a number of new individuals (fig. 236 N). In its life-cycle this genus thus closely follows *Phytodinium*, but the general resemblance to *Dissodinium* is unmistakable.

Order III. *DINOTRICHALES*

Up to the present only two filamentous members of Dinophyceae are known. One of these, *Dinothrix* (119), has so far only been found in marine aquaria. It has little-branched threads composed of a limited number (2–10) of barrel-shaped or rounded cells of large size; they are provided with stratified membranes, of which the innermost layer

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[1] This is the *Gymnodinium lunula* (later *Pyrocystis lunula*) of Schütt ((152), (153) p. 3) which was made the type of the genus *Diplodinium* by Klebs ((73) p. 390), the name being later changed to *Dissodinium*.

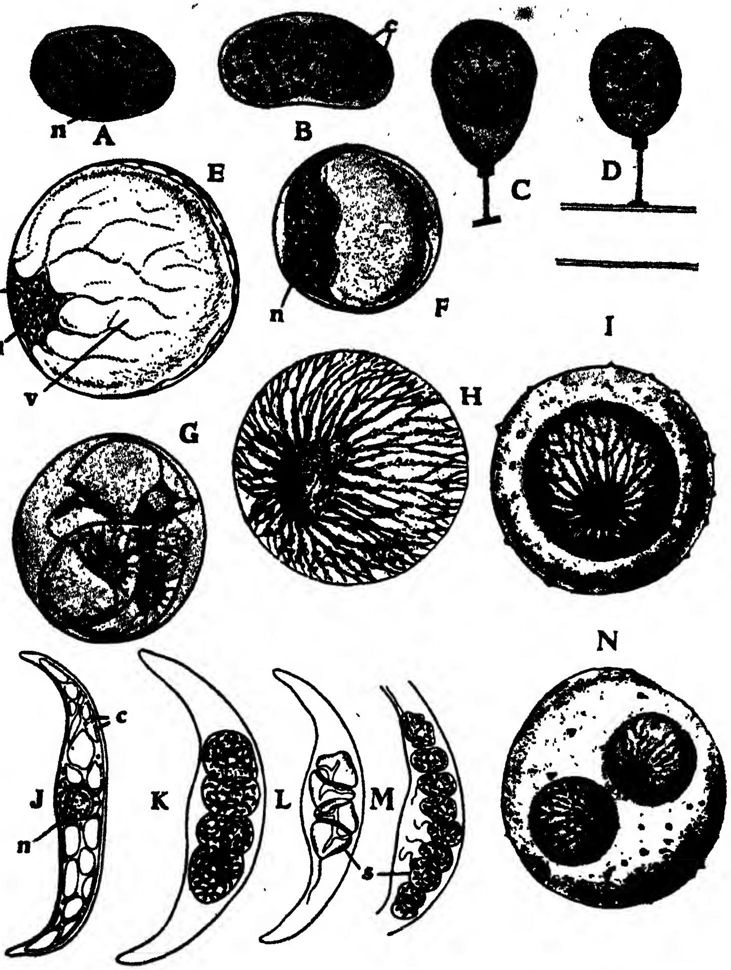

Fig. 236. Dinococcales. A, B, *Phytodinium simplex* Klebs; B, division-stage. C, D, *Stylodinium globosum* Klebs; C, liberation of protoplast from old parent-membrane. E–G, J–M, *Dissodinium lunula* (Schütt) Klebs; E, ordinary cell; F, commencement of division; G, formation of four daughter-cells; J, one of the lunate cells produced by further division of the latter; K, L, successive stages in formation of swarmers; M, formation of eight swarmers. H, I, N, *Pyrocystis Noctiluca* Murray; H, vegetative cell; I, the same with contracted protoplast; N, formation of two daughter-cells. *c*, chromatophore; *n*, nucleus; *s*, swarmer; *v*, vacuole. (A–D after Klebs; H, I, N after Murray; the rest after Dogiel from Oltmanns.)

at least consists of cellulose (fig. 237 A). The structure of the cells is altogether like that found in other algal Dinokontae (fig. 237 D), the large vacuole being traversed by numerous cytoplasmic strands which stretch from the local accumulation around the large excentric nucleus (*n*) to other parts of the parietal cytoplasm. In the latter the bulk of the discoid, yellow-brown chromatophores (*c*) are located; fat-drops (*o*) and small starch-like granules are also present. Some of the cells show a conspicuous red eye-spot.

In cell-division the protoplast contracts slightly and divides obliquely into two (fig. 237 G), the products ultimately coming to lie one in front of the other and each secreting a new membrane of its own. Protoplasts about to divide, as well as their division-products (fig. 237 H), commonly show an eye-spot (*s*) and sometimes exhibit distinct transverse and longitudinal furrows (*f*), in which case a stigma is always recognisable. Normally these gymnodinioid stages remain immotile and, after becoming enveloped by a membrane, lose the furrows and constitute ordinary cells of the filament. At times, however, a protoplast, after acquiring furrows and stigma, escapes without division through a hole in the wall (fig. 237 E) and acts as a zoospore (fig. 237 B, C). These swarmers are highly metabolic and very sensitive, perishing during observation so that it has been impossible to follow up their fate. Pascher, however, describes the finding of thin-walled cells with an eye-spot and others with a thicker stratified membrane, sometimes dividing, which he no doubt rightly regards as stages in the germination of the swarmers to form a new filament. He also describes palmelloid stages in which the cells of the filaments gradually fall apart; zoospores may likewise be produced from such stages.

Dinothrix is clearly a little-specialised form. All the cells are alike, there is no differentiation of apex and base, and every cell appears capable of division. The fact that essential features of the motile equipment (furrows, eye-spot) may appear during division also indicates that this form is but little removed from a motile ancestry.

In this connection it is of interest that the other member of Dinotrichales shows a much higher differentiation. *Dinoclonium* ((119) p. 15), discovered by Conrad, is an epiphyte (marine?) on other Algae and possesses a heterotrichous filament with prostrate and projecting threads (fig. 237 I), the latter unbranched and running out to a point. Reproduction is effected by gymnodinioid swarmers (fig. 237 F), apparently formed singly in the cells and escaping through a lateral aperture in the wall (fig. 237 I, *z*). The occurrence of this advanced type of plant-body among Dinokontae is significant and suggests that we are as yet only at the commencement of our knowledge of the filamentous Dinophyceae. Possibly some of the little-known filamentous Phaeophyceae may prove to belong here.

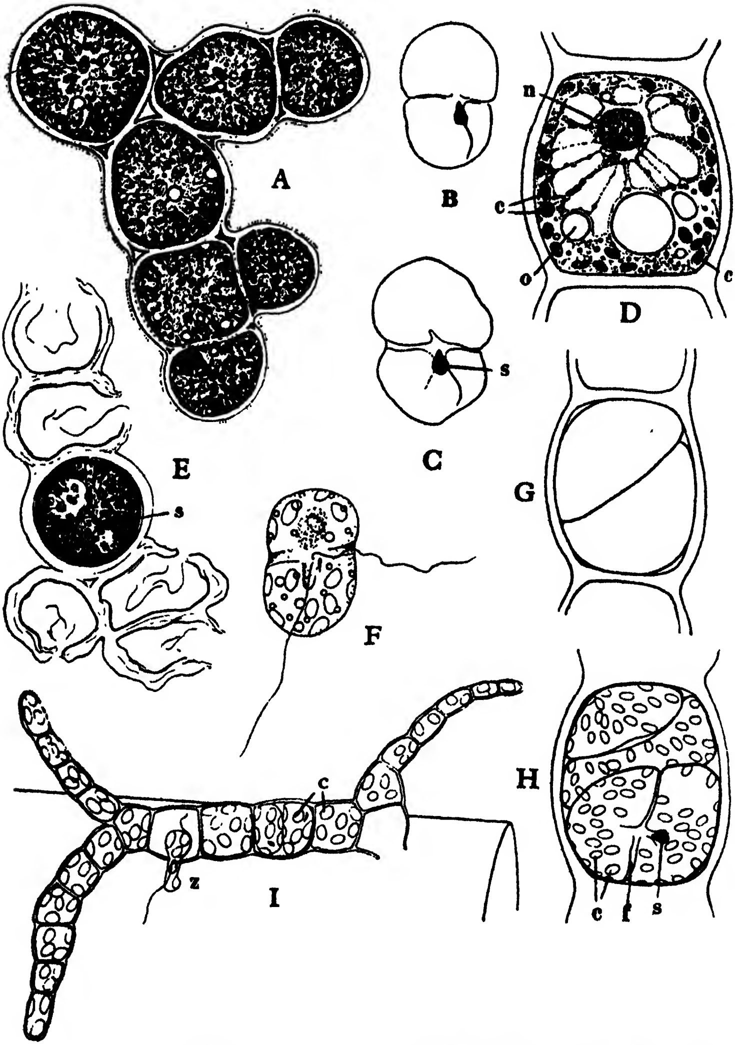

Fig. 237. Dinotrichales. A–E, G, H, *Dinothrix paradoxa* Pascher (after Pascher); A, seven-celled branched thread; B, C, two sketches of the same swarmer, showing metaboly; D, cell in optical section; E, six-celled thread from which all but one of the protoplasts have escaped; G, ordinary cell-division; H, the same with furrow-formation, etc. F, I, *Dinoclonium Conradi* Pascher (after Conrad from Pascher); F, swarmer. *c*, chromatophore; *f*, furrow; *n*, nucleus; *o*, oil; *s*, stigma; *z*, escaping swarmer.

THE INTERRELATIONSHIPS, AFFINITIES, AND CLASSIFICATION OF THE DINOPHYCEAE

It is a significant fact that in practically all the algal members of the Dinokontae reproducing by swarmers, these are of the *Gymnodinium*-type. This speaks strongly in favour of the view expressed on p. 688 of the primitiveness of the Gymnodiniaceae. Forms such as these must be regarded as the starting-points, not only for the numerous special developments seen among Dinoflagellata, but also for the line of algal evolution represented by Dinococcales and Dinotrichales. The difficulties in the way of directly relating them to the simpler members of the Desmokontae have already been fully discussed (p. 691); at present the gap between Desmokontae and Dinokontae, which are clearly related, remains unbridged.

As already mentioned at the outset of the consideration of the Dinophyceae, Pascher ((115), (119) p. 51) holds that Cryptophyceae, Desmokontae, and Dinokontae represent three divergent evolutionary lines from a common stock and groups them in the division Pyrrophyta, equal in rank with the Chlorophyta and Chrysophyta (cf. p. 642). He regards the Desmomonadaceae as the most primitive known forms of this division and suggests that the Cryptomonadales are derived from them by special development of the dorsiventrality and of the furrow-system which latter is regarded as being forshadowed in the apical incision of *Pleromonas* and *Haplodinium*. It must, however, be noted that we do not as yet understand the significance of the furrows in the protoplasts of Cryptomonads; they may not be fundamental and perhaps stress is being placed on a character of no great importance. Even without this, however, there is sufficient resemblance between *Haplodinium* and the Cryptomonads to warrant the assumption of a considerable degree of relationship. The similarity of pigmentation and assimilatory products is perhaps also significant.

A relationship between Dinoflagellata and Cryptomonadales has been emphasised by diverse authorities (73, 102). In particular it is profitable to compare the simpler members of the former with the Nephroselmidaceae (p. 657) among the latter. Such a form as *Hemidinium* shows considerable resemblances to *Protochrysis*. We may well be dealing with a large plexus of more or less closely related types, but too many of the significant genera are imperfectly known to be able to decipher the affinities clearly. For the present it is probably best to rank Cryptophyceae and Dinophyceae separately until a greater bulk of evidence as to their near relationship is forthcoming.

The relationship to Diatoms, which has in the past been assumed (153), can no longer be supported in the light of modern knowledge. Its main foundation lay in the bivalved character of the wall in the

Desmokontae, but this has really nothing in common with the complex envelope of Diatoms.

The following is a synopsis of the classification of the Dinophyceae, essentially based on Lindemann (102), Pascher (119), and Schiller (145):

A. *Desmokontae:*

(*a*) *Desmomonadales:*
1. *Desmomonadaceae:* Desmocapsa, Desmomastix, Haplodinium, Pleromonas.

(*b*) *Thecatales:*
2. *Prorocentraceae:* Exuviaella, Prorocentrum.

(*c*) *Dinophysiales:*
3. *Dinophysiaceae:* Dinophysis, Ornithocercus, Palaeophalacroma, Phalacroma, Thecadinium.
4. *Amphisoleniaceae:* Amphisolenia.

B. *Dinokontae:*

I. *Dinoflagellata:*

(i) *Peridinieae:*

(*a*) *Gymnodinioideae:*
5. *Pronoctilucaceae:* Entomosigma, Oxyrrhis, Pronoctiluca.
6. *Gymnodiniaceae:* Amphidinium, Cochlodinium, Gymnodinium, Gyrodinium.
7. *Polykrikaceae:* Polykrikos.
8. *Noctilucaceae:* Leptodiscus, Noctiluca.
9. *Warnowiaceae:* Erythropsis, Nematodinium, Proterythropsis, Warnowia.
10. *Blastodiniaceae:* Apodinium, Blastodinium, Oodinium, Paradinium, Paulsenella, Schizodinium.

(*b*) *Amphilothaloideae:* Amphilothus.

(*c*) *Kolkwitzielloideae:* Kolkwitziella.

(*d*) *Peridinioideae:*
13. *Glenodiniaceae:* Bernardinium, Glenodinium, Hemidinium.
14. *Protoceratiaceae:* Protoceratium.
15. *Gonyaulaceae:* Gonyaulax, etc.
16. *Peridiniaceae:* Acanthodinium, Diplopsalis, Heterocapsa, Peridinium.
17. *Ceratiaceae:* Ceratium.
18. *Goniodomaceae:* Goniodoma.
19. *Ceratocoryaceae:* Ceratocorys.
20. *Podolampaceae:* Podolampas.

(ii) *Dinocapsineae:*
21. *Dinocapsaceae:* Gloeodinium.

(iii) *Rhizodinineae:* Dinamoebidium.

II. *Dinococcales:*

23. *Dinococcaceae:* Cystodinium, Dinastridium, Dissodinium, Hypnodinium, Phytodinium, Pyrocystis, Stylodinium, Tetradinium.

III. *Dinotrichales:*

24. *Dinotrichaceae:* Dinothrix.

25. *Dinocloniaceae:* Dinoclonium.

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Class VII. CHLOROMONADINEAE

As far as our present knowledge goes, this is but a very small class comprising a few highly specialised, unicellular, flagellate types of relatively large dimensions, none of which has yet been adequately studied (7). They tend to be mud-forms or frequent waters with abundant larger aquatics, but rarely occur in quantity. Unlike the Chrysomonadales or Cryptomonadales no simply organised motile forms are known, nor have any palmelloid or coccoid representatives so far come to light.

Vacuolaria virescens (1, 3, 5) (*Coelomonas grandis* Stein (10)) is the form most frequently encountered and may be taken as a typical example. The naked ovoid or pear-shaped cells are slightly dorsiventral, with a rounded posterior and a narrower anterior extremity (fig. 238 A). The periplast is delicate and the cells are highly metabolic. They possess two equal, apically inserted flagella arising from a slight depression; one flagellum is directed forwards, while the other trails behind along the ventral surface which often exhibits a distinct groove. The movements are slow and are accompanied by continuous rotation. There is no eye-spot. The numerous discoid chromatophores, found in all pigmented Chloromonadineae, have a bright green tint of a different shade to that of the Xanthophyceae, but here as there due to an excess of xanthophyll, so that a blue-green colour is obtained with hydrochloric acid. Food-reserves are stored as fat.

The large nucleus (fig. 238 A, *n*) lies above the middle of the body. Contractile vacuoles are found at the anterior end and seem to arise as a number of small vesicles (fig. 238 B, C, *v*) which gradually unite to form one or two larger ones, the latter probably discharging their contents direct to the exterior. Reproduction is effected by longitudinal division of individuals which have come to rest and have become enveloped in copious mucilage. Spherical cysts with a thick envelope of mucilage are also known.

Trentonia (8, 11, 12) is less markedly metabolic and has an obliquely truncated anterior and a pointed posterior end (fig. 238 D). At the apex of the cell is a large non-contractile reservoir (*r*), triangular in shape in optical section and communicating with the exterior by a narrow canal; adjacent to it, and probably discharging into it, is a single contractile vacuole (*v*). *Gonyostomum* ((4), (9); *Raphidomonas* Stein (10)) shows the same feature and, like *Trentonia*, has flattened dorsiventral cells (fig. 238 E–G). The peripheral cytoplasm here, however, contains numerous strongly refractive rod-like bodies (*t*) which are radially arranged. These appear to be trichocysts which under the influence of external stimuli become protruded as long threads.

Two colourless forms are known. In *Thaumatomastix* (6) the cells are broadly ovate and the delicate periplast bears numerous short bristles (fig. 238 K, *b*). In this case the backwardly directed flagellum is twice as long as the other, being as usual located in a ventral furrow (*fu*). The two contractile vacuoles (*v*) at the front end discharge alternately into the apical vesicle (*r*). The cells are markedly flattened and the ventral surface is protruded into a number of radiating rhizo-

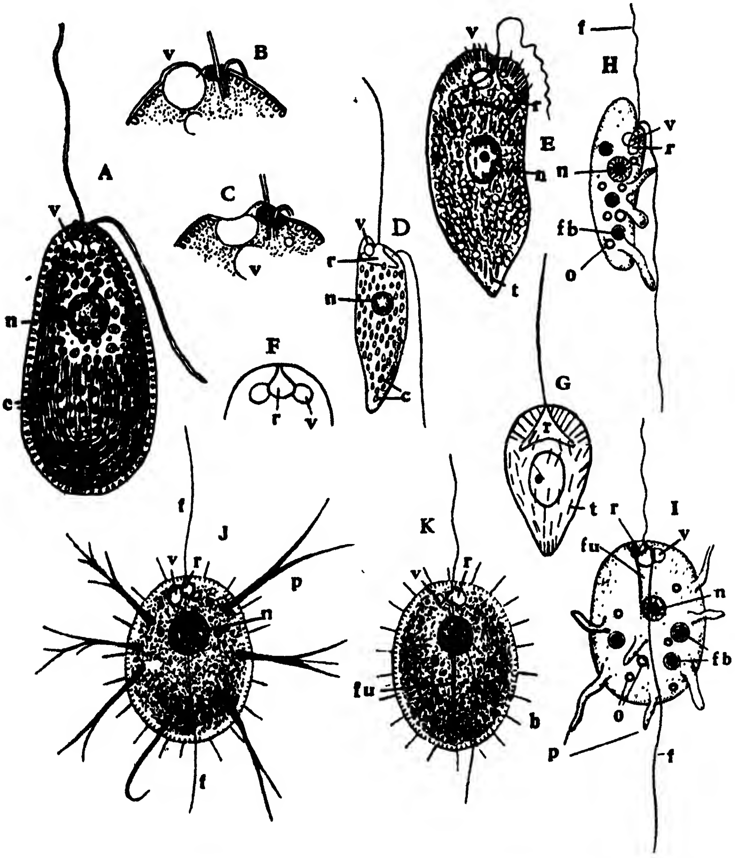

Fig. 238. Chloromonadineae. A–C, *Vacuolaria virescens* Cienk. (after Senn); B, C, enlarged anterior extremity to show vacuolar system. D, *Trentonia flagellata* Stokes (after Stokes). E–G, *Gonyostomum semen* Dies. (E after Stein; F, G after Malins Smith); F, the vacuolar system. H, I, *Reckertia sagittifera* Conr. (after Conrad); H from the side and I from the ventral surface. J, K, *Thaumatomastix setifera* Lauterb. (after Lauterborn); J with rhizopodia. *b*, bristles of periplast; *c*, chromatophore; *f*, flagellum; *fb*, food-bodies; *fu*, furrow; *n*, nucleus; *o*, oil-drops; *p*, pseudopodia; *r*, reservoir; *t*, trichocysts; *v*, contractile vacuoles.

podia (fig. 238 J, *p*) which are branched and very mobile and probably play a rôle in holozoic nutrition.

Conrad's *Reckertia* (2) has markedly flattened cells (fig. 238 H, I) with a furrow (*fu*) confined to the anterior part of the ventral surface. The peripheral cytoplasm, as in *Gonyostomum*, contains numerous trichocysts, but the ready protrusion of pseudopodia (*p*) recalls *Thaumatomastix*. There are two contractile vacuoles (*v*) at the anterior end which discharge into a single vesicle (*r*).

Nothing is known of the reproduction of any member of the class except *Vacuolaria*. Owing to the pigmentation of the chromatophores and the presence of oil an affinity with the Xanthophyceae has been assumed, but there is no other evidence pointing in that direction and it would be very difficult to attach the Chloromonadineae to the Heterochloridales. In a few respects there are resemblances to the Euglenineae, viz. in the character of the chloroplasts and in the vacuolar apparatus, but the absence of paramylon and other features render any close affinity improbable. The presence of a ventral furrow harbouring part of the backwardly directed flagellum recalls the classes just discussed. At present the Chloromonadineae are best regarded as an isolated class of uncertain relationships.

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Class VIII. EUGLENINEAE

The Euglenineae are another class of highly differentiated, naked Flagellates whose origin is obscure. The members show a more definite trend in the direction of animal organisation than is found in most of the classes of pigmented Protophyta. In fact, in many representatives of the colourless Peranemaceae, holozoic nutrition is the rule and the individuals are specially equipped for this purpose. It is possible that the future may show the existence of algal derivatives, but the bulk of the Euglenineae are so specialised that this appears little likely. Schiller (91) has, however, described some relatively unspecialised forms from the Adriatic (cf. p. 732) and expresses the opinion that the sea will afford further examples of such simple types.

There is no doubt, however, that the chief home of the Euglenineae is in freshwaters where they often play a considerable rôle, especially in waters rich in organic nutriment or which harbour abundant plant-growth. Not uncommonly they occur in such numbers as to give a characteristic coloration to the water, green for example in the case of *Euglena viridis* Ehrenb., red in the case of *E. sanguinea* Ehrenb., or brown as in that of species of *Trachelomonas* (62, 78–80, 105). A number of species of *Euglena* inhabit damp mud, and *E. limosa* plays an important part on the banks of estuaries or on salt-marshes ((9), (10), (15) p. 201, (41)), often colouring the mud over wide stretches and showing a periodicity in its appearance at the surface related to the tides.

The General Characteristics of the Euglenineae[1]

In the ordinary state the individuals are usually motile with the help of one (fig. 239 B, D, G, N) or two (*Eutreptia*, fig. 239 F; *Heteronema*, fig. 242 A; *Entosiphon*, fig. 242 I) rather thick flagella, which are of very diverse length and inserted apically.

The accounts of their structure are somewhat contradictory, but it seems that they are composed of an elastic axial thread (sometimes excentric) surrounded by a contractile envelope of alveolar cytoplasm from which the end of the axial thread may project (53). The fine unilateral lashes (cilia) described by Fischer (37) on the flagellum of *Euglena viridis* are found also in *Phacus pleuronectes*, but do not appear to be general in the Euglenineae (73). According to Dellinger (28) the flagellum of *Euglena* consists of four fibrils twisted about one another,

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[1] See (18–20), (27), (63), (64), (96).

while he considers Fischer's cilia to be artefacts (see also p. 32). The flagella, owing to their thickness, are easily seen in the living organism, but are frequently cast off at death and are therefore commonly lacking in preserved material.

The single flagellum, as well as the two found in *Eutreptia*, are directed forwards (fig. 239), but in most forms possessing two flagella the second, which may be longer or shorter, trails behind during movement (fig. 242 A, I). In *Gymnastica* ((91) p. 96) the second flagellum is very short (fig. 239 E). While many Euglenineae swim freely, others chiefly exhibit a creeping movement in contact with some substratum (e.g. Peranemaceae; some *Euglenas*, such as *E. deses*).

The shape of the individuals is very diverse. They are often approximately round in cross-section (*Euglena*, *Lepocinclis*, fig. 239 N), though very prominently flattened in *Phacus* (fig. 239 I, J). The periplast is relatively soft in many species of *Euglena*, as well as in *Trachelomonas*, and in such cases the individuals during life show very marked metaboly, especially at times when active movement with the help of the flagellum is not taking place. Many Euglenineae (*Lepocinclis*, fig. 239 M, N; *Phacus*; many *Euglenas*), on the other hand, have a rigid periplast that does not admit of change of shape. In these it frequently exhibits a characteristic longitudinal or spiral striation (cf. (67) and fig. 239 H–J), while in *Phacus*, according to Deflandre (26), there are often fine transverse striations between the longitudinal ones; in *P. costata* (11) the periplast is stated to be detached from the rest of the protoplast opposite the spiral ribs. In certain *Euglenas* the rigid periplast bears rows of small warts (*E. Spirogyra*, fig. 239 C) through which according to Klebs (63) and Mainx ((72); cf. also (22)) secretion of mucilage, which may even surround the motile individual, takes place. The posterior end of the cell is commonly drawn out into a more or less sharply demarcated point or spine (fig. 239 C, H–J, N). Jirovec (57), by means of the silver precipitation method, has demonstrated the presence of a system of somewhat spirally arranged fibrils in the periplast, similar to that found in various Volvocales (cf. p. 32). The protoplast harbours numerous small vacuoles (21, 22, 49).

A large number of the Euglenineae lack chromatophores, but in the holophytic Euglenaceae there are mostly several or even numerous chloroplasts which are of a pure green colour. In shape they are usually either discoid (fig. 239 B, I), lobed (fig. 240 A), or band-like, the bands being occasionally arranged in one (*Euglena viridis*, fig. 239 G) or more (*E. oblonga*) characteristic stellate groups (92). In some species of *Trachelomonas*, as well as in *Cryptoglena* (fig. 241 E), there are two curved plate-shaped chloroplasts. The exact nature of the pigments has not been determined and, while according to Baas-Becking (4) the absorption-spectrum of *Euglena* is not unlike that of

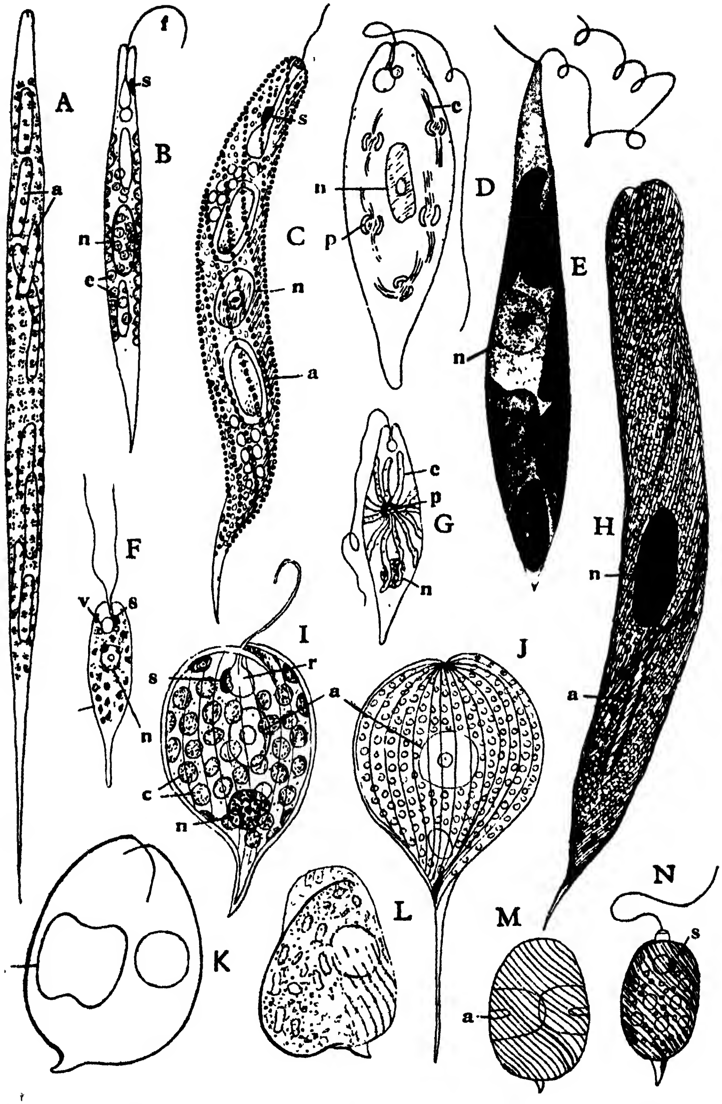

Fig. 239. Types of motile Euglenaceae. A, B, *Euglena acus* Ehrenb. C, *E. Spirogyra* Ehrenb. D, *E. polymorpha* Dang. E, *Gymnastica elegans* Schill. F, *Eutreptia viridis* Perty. G, *Euglena viridis* Ehrenb. H, *E. oxyuris* Schmarda. I, *Phacus pleuronectes* (O. F. M.) Duj. J, *P. longicauda* (Ehrenb.) Duj.

higher green plants, Günther (46) states that the chlorophyll is spectroscopically different. In a few species (*Euglena sanguinea*, etc.) the cells are coloured red by haematochrome.

The products of assimilation appear as solid, often large granules of *paramylon*[1] of very diverse shape (discs; rods, fig. 239 A, B, H; rings, fig. 239 J, M; grains shaped like a cottage-loaf, fig. 239 K, etc.). The shape is generally constant for the species, but in some cases small ring-shaped grains become solid as they enlarge ((17) p. 213). Paramylon is a polysaccharide which fails to stain with iodine or chlor-zinc-iodide, is insoluble in boiling water, but dissolves both in concentrated sulphuric acid and in potash; formalin often brings about a gradual solution. When the grains are subjected to dilute (6 per cent.) potash they swell and then often exhibit a concentric stratification (sometimes visible without special treatment) like that of starch-grains (fig. 240 C, D), which they also resemble in being doubly refractive. The central portion of the grains appears to be less dense than the peripheral.

The paramylon-grains always originate in the cytoplasm (cf. however (30)), but in many species of *Euglena* they develop in apposition to the chloroplasts, although in other cases (e.g. *Phacus*, *Lepocinclis*) there is apparently no such relation. Where the grains are large and show a definite shape and orientation (as in fig. 239 C, J, M) it must be assumed that they originate around special cytoplasmic centres which are sometimes distinguishable (*E. deses*, *viridis*) and have been wrongly termed pyrenoids (cf. (17) p. 211, (73)). Whilst the grains undoubtedly increase in size or number during active photosynthesis and decrease during starvation, the large characteristically shaped grains especially would in many cases appear to possess a rather marked degree of persistence.

In several species of *Euglena* and *Trachelomonas* the chloroplasts possess a so-called *pyrenoid* which consists of two hemispherical portions projecting prominently from either surface (figs. 239 D; 240 A, B). Such pyrenoids are either naked or provided on the outer side (*E. pyrum* Klebs), or on both sides, with a sheath of paramylon having the shape of a watch-glass (cf. fig. 240 A, B, *a*). According to Mainx (73) the paramylon may become detached and lie as free grains in the cytoplasm, while a new sheath is deposited on the pyrenoid.

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[1] See (14), (17) p. 210, (19), (68), (92).

K, L, *P. anomala* Fritsch and Rich; L, oblique view showing the keel. M, N, *Lepocinclis ovum* (Ehrenb.) Lemm. *a*, paramylon-grains; *c*, chloroplasts; *f*, flagellum; *n*, nucleus; *p*, pyrenoid; *r*, reservoir; *s*, stigma; *v*, contractile vacuole. (A after Deflandre; B after Klebs; D after Dangeard; E after Schiller; H, M after Fritsch; I after Senn; K, L after Fritsch & Rich; N after Stein; the rest after Lemmermann.)

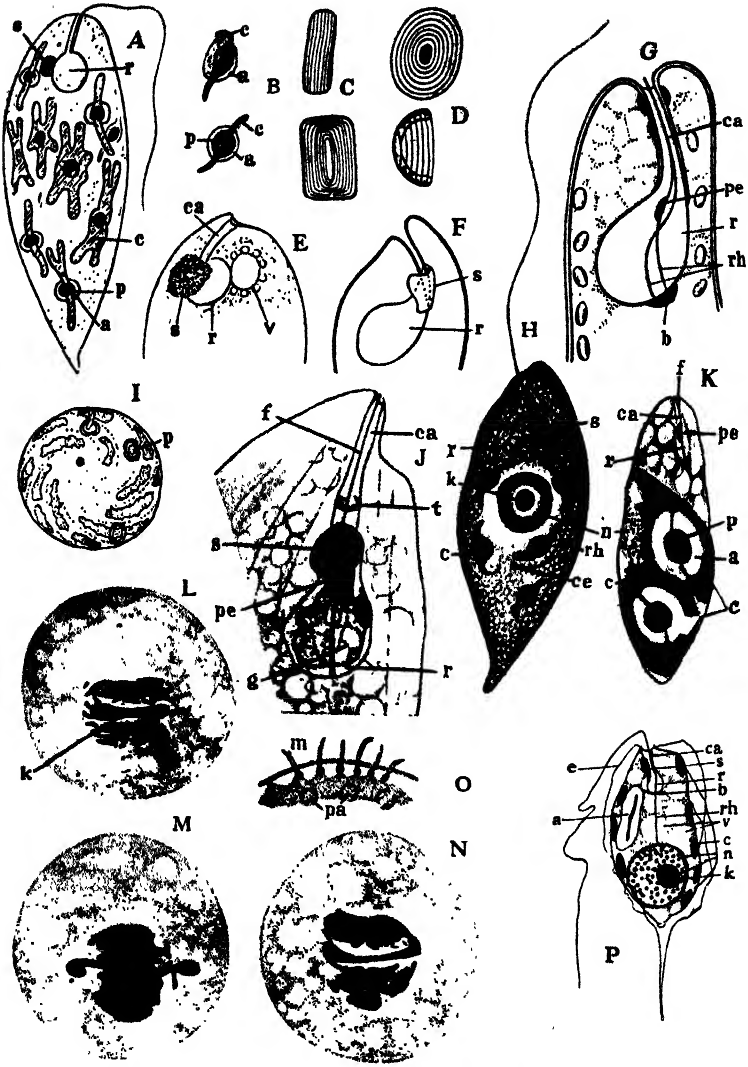

Fig. 240. General organisation of the Euglenaceae. A, D, O, *Euglena velata* Klebs; D, paramylon-grains, the lower in profile; O, part of surface in section showing relation between mucilage-threads and the peripheral dilations of the protoplast. B, *E. granulata* (Klebs) Lemm., two chromatophores in optical section with pyrenoids (*p*) and paramylon-sheath (*a*). C, E–G,

In *E. mucifera* Mainx (72) the pyrenoids are borne on special short processes on the inner surface of the chloroplast (fig. 240 I, *p*). It does not appear that the pyrenoids of Euglenineae possess the fluid consistency of those of Chlorophyceae, since in fixed material they do not show the clear surrounding area seen in the latter (cf. (17) p. 212). Many Euglenineae also store fat-globules as a food-reserve.

The *vacuolar system* is usually complex. The periplast is invaginated at the anterior end to form a short narrow canal (102) leading down to and communicating with a large and prominent vacuolar reservoir (fig. 240 E–G, J, *r*). In certain cases the canal, just above the point where it passes into the reservoir, shows a ring-shaped thickening (fig. 240 J, *t*) (cf. (46), (53), (55) p. 19) which has been interpreted as a sphincter serving to close and open the canal. It is probable that the periplast does not always line the whole of the latter. Sigot (97) records the presence of numerous bodies staining with osmic acid around the canal in *Euglena gracilis*. Near the reservoir are one (e.g. *Phacus pleuronectes*, *Euglena Ehrenbergii*, fig. 240 E) or more (*E. deses*) large vacuoles (*v*) which sooner or later fuse with the reservoir, after which the latter gradually contracts to its original dimensions, no doubt discharging into the canal (*ca*). During the gradual enlargement of the contractile vacuole a rosette-like group of minute accessory vacuoles (cf. fig. 240 E) appears around its periphery and, as the former fuses with the reservoir, the members of the rosette unite to form a new vacuole. A much simpler vacuolar system has been described by Schiller (91) for certain marine forms (p. 732). In many Euglenineae there is situated adjacent to the reservoir a prominent eye-spot (55, 102) (fig. 240 E, J, *s*) about whose morphological nature there has been much discussion (see (45), (49), (74) and p. 730).

The flagella emerge from the canal (fig. 240 A, P) and appear normally to extend back to the posterior end of the reservoir (fig. 240 G). In diverse Euglenineae (*Euglena*, *Astasia*) the single flagellum

E. Ehrenbergii Klebs; C, paramylon-grains, the upper in profile; E–G, anterior end enlarged to show vacuolar apparatus and associated structures. H, *E. sanguinea* Ehrenb. I, *E. mucifera* Mainx, rounded individual, stalked pyrenoids (*p*). J, *Phacus pleuronectes* (O. F. M.) Duj., anterior end. K, *Euglena pisciformis* Klebs, stained individual. L–N, *E. viridis* Ehrenb., successive stages in nuclear division. P, *Phacus caudata* Hübner, stained individual. *a*, paramylon; *b*, basal granule; *c*, chloroplast; *ca*, canal; *ce*, centrosome; *e*, periplast; *f*, flagellum; *g*, gullet; *k*, caryosome; *m*, mucilage-thread; *n*, nucleus; *p*, pyrenoid; *pa*, paramylon groups; *pe*, photoperceptor; *r*, reservoir; *rh*, rhizoplast; *s*, stigma; *t*, thickening of wall of canal; *v*, contractile vacuole. (A after Dangeard; B after Schmitz; D after Bütschli from Oltmanns; F, G after Hamburger; H after Haase; I after Mainx; J, K after Haye; L–N after Tschenzoff; P after Bretschneider; the rest after Klebs.)

has been shown to fork on entering the reservoir (fig. 240 G, H),[1] the two forks terminating in one (53) or two basal granules. It appears, however, that such forking does not normally occur in *Phacus* (fig. 240 P), *Trachelomonas*, or *Menoidium* ((11), (73) p. 312, (84); cf. however (50)). In some species (*E. sanguinea* (47)) the forks are prolonged into the body of the cell and terminate in a common granule, probably a centrosome, posterior to the nucleus (fig. 240 H, *ce*), whilst in other cases (5, 11, 87) a rhizoplast extends from the basal granule or from one of them up to the nuclear membrane where it ends in a similar granule (fig. 240 P). An extension of the base of the flagellum beyond the floor of the reservoir has, however, by no means been universally recorded (cf. e.g. (69)). In *Eutreptia* (98) the two flagella are united by a horseshoe-shaped mass of denser cytoplasm at the base of the reservoir. The fact that the single flagellum is commonly double in its basal part perhaps indicates that the biflagellate condition is primitive in the Euglenineae.

Various workers have reported a thickening of the flagellum or of one of its branches in the neighbourhood of the stigma (fig. 240 G, J, *pe*) and, according to Haye ((55) p. 21), this is a separate cylindrical mass which he regards as a photoperceptor. Mast ((75) p. 215) concludes that the latter represents part of the stigma which has divided into two, the main portion containing only shading pigments, while the photoperceptor includes the light-sensitive part (cf. also (4*a*) p. 455, (73)).

The *nucleus* is usually large and prominent and exhibits a central caryosome (fig. 240 H, P, *k*) with a surrounding chromatin reticulum. The chromatin sometimes shows a radial arrangement (1, 60), but this is possibly a condition marking the early prophase of division. In *Heteronema* (69) the caryosome is frequently fragmented. The process of nuclear division has been abundantly studied and is characterised by the absence of a spindle and by the persistence of the caryosome. The latter becomes drawn out in a direction perpendicular to the plane of division, assuming more or less of the form of an hour-glass (fig. 240 L–N), while the chromosomes become aggregated about its middle and ultimately separate into two groups about its two halves (figs. 240 N; 243 J) (see (1), (19), (60), (65), (101)).

Tschenzoff (101) concluded that in *E. viridis* the chromosomes underwent splitting during the anaphase or telophase of the previous division, retaining their individuality during the resting phase, but becoming grouped in pairs at the next metaphase and then separating. According to Drezepolski (31) the chromosomes show various stages of differentiation among the species of *Euglena*. Schüssler (94) states that the chromosomes are formed from the caryosome in *Scytomonas*, of which at present there is no confirmation.

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[1] See (12), (50–53), (73), (102).

The recent study by Baker(5) of nuclear division in *E. gracilis* (=*E. agilis* Carter) appears to afford considerable evidence of the existence of an intranuclear centrosome lodged in the caryosome; from this centrosome the basal granules of the flagella are derived (cf. p. 730). At the commencement of nuclear division according to Baker the centrosome emerges from the caryosome (fig. 243 H, I, *ce*) and takes up a position adjacent to the nuclear membrane where it divides (cf. also (7)). During the division of the nucleus, which at this stage lies near the reservoir (fig. 243 I, J), the two halves of the centrosome (*ce*) separate. Each cuts off a granule that passes to the wall of the reservoir and constitutes the basal granule of the flagellum. This remains connected with the centrosome by a rhizoplast (fig. 243 J, *rh*). Each basal granule divides and from the two granules the two flagellar roots originate; one of these remains short and fuses with the other, so that the above-described forking is seen only in the lower part of the flagellum. The flagellum of the parent-individual with its two basal granules is absorbed into the protoplast. Later the rhizoplast disappears, but according to Baker the centrosome remains recognisable as a small granule in the cytoplasm up to the time of the next nuclear division.

Much the same is described for other species of *Euglena*(47, 58, 88), *Trachelomonas*(104), *Menoidium*(48), *Scytomonas*(8), and *Peranema*(52), although in most cases only extranuclear centrosomes are recorded. Various workers have expressed doubts as to the reliability of the evidence furnished by Baker for the intranuclear origin of the centrosome (cf. (52)). It seems that in all the cases just mentioned flagella are formed *de novo* on the daughter-individuals from basal granules that originate by the division of centrosomes, although in *Entosiphon*(65) and *Heteronema*(69) the two flagella are stated to be retained by one daughter-individual, while their basal granules divide and give rise to the two flagella of the other individual. In *Scytomonas*, too, Dobell(29) and Schüssler(94) affirm a division of the basal granules of the old flagella to form those of the new ones, while Berliner's account(8) is in conformity with that of Baker and others. Various recent investigators have failed to find centrosomes(43, 65).

THE HOLOPHYTIC FORMS (EUGLENACEAE)

The holophytic forms are generally grouped in the single family Euglenaceae, among which Mainx ((73) p. 350) regards the biflagellate *Eutreptia* (fig. 239 F) as the most primitive member. In *Gymnastica* (fig. 239 E) there are likewise two flagella, but of markedly different length. The uniflagellate type in its simplest form is illustrated by *Euglena* (fig. 239 A–D, G, H), although many of its species show considerable specialisation and lead over to the closely allied *Lepo-*

cinclis (38, 64, 108) (fig. 239 M, N). A number of species of *Euglena* seem always to lack the flagellum (34) and exhibit only amoeboid movements. Elenkin (35) suggests that they illustrate a similar amoeboid tendency to that noted in other classes (cf. especially Chrysophyceae). Pascher (80 *a*) has described an amoeboid form provided with a stigma and inhabited by *Zoochlorellae* which he suspects of being a colourless euglenoid type.

The markedly flattened individuals of *Phacus* ((11), (39) p. 73) (fig. 239 I–L) have a rigid periplast which is often longitudinally or spirally striated, the striations sometimes bearing spines or warts. One surface is commonly slightly convex, the other slightly concave, and the cells are occasionally twisted and of complex shape. In a number of species the periplast is provided with a fold (keel) running more or less longitudinally over part or over the whole of the convex dorsal surface (fig. 239 L).

Of the simple marine forms described by Schiller (91), *Chlorachne* has strongly metabolic, rather small cells possessed of a delicate periplast (fig. 241 A). There appears to be no anterior invagination, the long band-shaped flagellum arising directly from the anterior extremity, while beneath its point of insertion are two contractile vacuoles. Here there are numerous chloroplasts, but in the otherwise similar *Ottonia* (fig. 241 B) there are only two lateral ones; no data are available as to the vacuolar system of this form. It is to be hoped that a better knowledge of these simple types will soon be obtained, since they may well afford data as to the affinities of the whole class.

In all the Euglenaceae hitherto mentioned the individuals are naked, but in the freshwater *Trachelomonas* (fig. 241 C, D, M), as well as in *Ascoglena* (fig. 241 I) and others, they are enclosed in a special envelope separated from the protoplast by a well-marked space and provided with an apical aperture for the emergence of the flagellum. In the biflagellate *Amphitropis* (42) the envelope is winged and the flagellar aperture is provided with a collar. These are thus encapsuled types, parallel with Phacotaceae among Chlamydomonadineae and with *Chrysococcus*, etc. among Chrysomonadineae, and in *Cryptoglena* ((64) p. 355), where the close-fitting envelope is composed of two halves (fig. 241 E, F) apposed to the broader faces of the flattened cell, the analogy with *Phacotus* is specially marked.

The individuals of *Trachelomonas* are free-swimming and the envelope is rigid, very diverse in form (fig. 241 C, D), and often provided with variously disposed outgrowths. At first it is hyaline, but later is generally coloured yellow, brown, or dark brown by iron-salts and it may completely obscure the contained protoplast. The flagellar aperture is relatively narrow, the rim often being thickened or produced as a cylindrical collar (fig. 241 D). It would seem that in some cases at least the shape and size of the envelope may be subject to great varia-

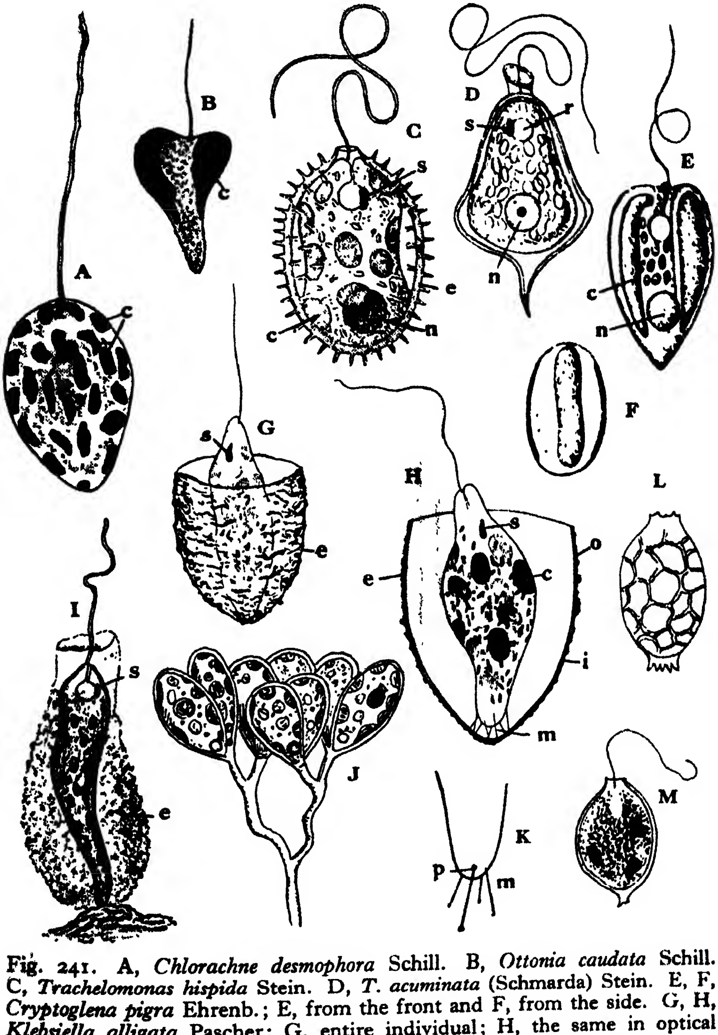

Fig. 241. A, *Chlorachne desmophora* Schill. B, *Ottonia caudata* Schill. C, *Trachelomonas hispida* Stein. D, *T. acuminata* (Schmarda) Stein. E, F, *Cryptoglena pigra* Ehrenb.; E, from the front and F, from the side. G, H, *Klebsiella alligata* Pascher; G, entire individual; H, the same in optical section. I, *Ascoglena vaginicola* Stein. J, *Colacium arbuscula* Stein. K, *Euglena terricola* (Dang.) Lemm., posterior end with pore (*p*) and mucilage-threads (*m*). L, M, *Trachelomonas inconstans* Carter; L, envelope; M, a living individual. *c*, chloroplasts; *e*, envelope; *i*, inner and *o*, outer parts of same; *m*, mucilage-threads; *n*, nucleus; *r*, reservoir; *s*, stigma. (A, B after Schiller; C after Senn; E, F after Lemmermann; G, H after Pascher; K after Günther; L, M after Carter; the rest after Stein.)

tion(44) and the innumerable species at present established on the characters of the envelope alone are hardly likely to be warranted.[1]

Ascoglena is an epiphyte in which the individuals are attached by their posterior ends to the base of a cylindrical or urn-shaped roomy envelope which is of soft texture, yellow or brown in colour in older individuals, and provided with a wide flagellar aperture (fig. 241 I). Pascher's *Klebsiella*(81), a marine free-swimming form, has a similar wide and soft envelope, from which the euglenoid individual may project somewhat (fig. 241 G, H). Both here and in *Ascoglena* the envelope consists of an inner hyaline layer (*i*) and an outer one (*o*) impregnated with iron-compounds. In *Klebsiella* the posterior end of the individual is attached to the base of the envelope by a number of delicate and elastic, gelatinous threads (fig. 241 H, *m*). The manner of attachment is similar to that described by Günther(46) for a number of species of *Euglena* (e.g. *E. terricola*, fig. 241 K) which temporarily fix themselves to a substratum or to one another by their posterior extremities. The attaching threads in this case are secreted through definite pores (*p*) situated around the posterior end of the individual, one being considerably larger than the others, and similar pores are likely to be present in *Klebsiella*. The mode of attachment of the individual to the envelope in *Trachelomonas* and *Ascoglena* remains to be investigated. Temporary formation of an envelope has also been recorded in *Euglena chlamydophora* by Mainx(73) where it arises in connection with encystment (p. 740).

A rather different habit is seen in the colonial *Colacium* ((63) p. 321, (90)), usually found on freshwater plankton-organisms, especially Copepods.[2] The individuals are here devoid of flagella and are situated at the ends of simple or branched mucilage-stalks, generally forming small dendroid colonies (fig. 241 J). The cells are provided with a thin mucilage-envelope and multiply by longitudinal division. A flagellum is only acquired in connection with reproduction.

The Saprophytic Forms

The Euglenaceae, despite their chloroplasts, no doubt possess saprophytic tendencies and, as in the case of other heterotrophic forms, the various species differ in their requirements with respect to organic food. Mainx ((73), cf. also (33)) finds that the forms investigated by him can live a purely autotrophic life, both as regards

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[1] Deflandre(25) has placed a considerable number of the species in a new genus *Strombomonas* distinguished chiefly by the absence of a demarcated collar around the base of the flagellum and by certain differences in the structure of the envelope.

[2] A species of this genus, epiphytic on Algae, has recently come to my notice.

carbon and nitrogen, but that all can also derive their nitrogen from amino-acids. *Euglena gracilis* (100), *Phacus pleuronectes*, and *Colacium vesiculosum* were found to be capable of satisfying their carbon-requirements from the same source (see also (71)), but this was not true of the other Euglenaceae examined. According to Lwoff and Dusi (32, 70, 107) most species of *Euglena* (*E. pisciformis*, *deses*, *Klebsii*), while in part requiring organic nitrogen, can only multiply in the light since they can obtain their carbon solely from the carbon dioxide of the air in the process of photosynthesis. On the other hand *Euglena gracilis* (100, 106), and perhaps other species as well, only thrive when carbon in an organic form is available, while Cunningham and Hearne (16) found that *E. tripteris* multiplied more rapidly in the absence of carbon dioxide.

Other indications of saprophytism are not lacking. Diverse green (and colourless) members of Euglenineae are known to occur in the alimentary tracts of frogs and tadpoles (2, 6, 103)[1] and Hegner (56) states that if frogs are strongly infected they are dwarfed. Various colourless Euglenaceae are known, e.g. *Euglena quartana* Moroff (77), *E. acus* var. *hyalina* Klebs ((63) p. 311) and var. *pallida* Dangeard (23), *Phacus pleuronectes* var. *hyalina* ((63) p. 313), and *Trachelomonas reticulata* Klebs ((63) p. 322), the last but one sometimes occurring in enormous numbers in old impure cultures.

Euglena gracilis, when grown in culture-solutions in the dark, loses its pigment, although retaining its plastids, and on exposure to light the latter again become green ((106); cf. also (93)). Reduction of chloroplasts and loss of pigment, however, also occur when abundant nutriment is available or as the result of nitrogen-starvation (86). At times of saprophytic nutrition the pyrenoids disappear and the paramylon is produced in the cytoplasm (4a). It has further been shown that in culture individuals of *E. gracilis* can appear that lack plastids altogether and are therefore permanently colourless. Ternetz (100) has suggested that this is due to one of the chloroplasts of a given individual losing the capacity for division, so that after a certain number of generations some of the offspring would be colourless (cf. Chrysophyceae, p. 541). According to Tannreuther (99) *Euglena* may exhibit holozoic nutrition.

The diverse tendencies just discussed may indicate the mode of origin of the saprophytic Astasiaceae[2] which are usually found in stagnant waters rich in decaying vegetable matter, as well as in polluted water. All the known members are free-swimming and, except for the absence of chloroplasts, show much resemblance to the Euglenaceae, paramylon being again the reserve-food. Some possess a single

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[1] Wenrich (103) refers some of these forms to a distinct genus, *Euglenamorpha*, but the several flagella present are probably indicative of rapid multiplication (cf. (50)).

[2] See (13), (19), (35a), (59), (61), (63), (64), (83), (96).

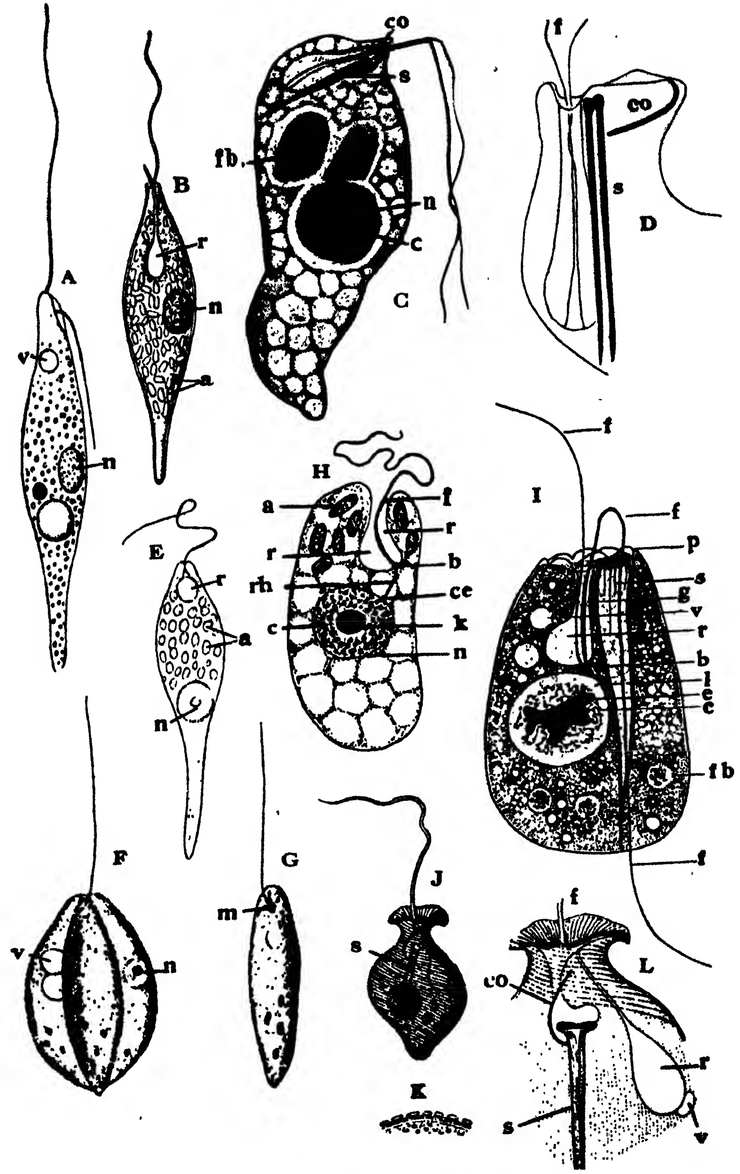

Fig. 242 [*for description see opposite*]

flagellum (*Astasia*, fig. 242 E; *Menoidium*, fig. 242 H), others have two unequal ones (*Distigma*, fig. 242 B). An eye-spot is rarely present. In *Astasia* and *Distigma* the individuals show pronounced metaboly, while in *Menoidium*, in which the cell is more or less curved, sometimes even S-shaped, the periplast is firm and in most cases longitudinally striated. Diverse species of *Astasia* live in animal intestines (2, 6).

THE HOLOZOIC FORMS

The members of the third family, the Peranemaceae,[1] exhibit mainly holozoic nutrition and, in some genera, the protoplast includes a special rod-shaped organ or *siphon* which has been credited as acting as a kind of suction-pump, although in a considerable number such a structure is lacking. Species of *Scytomonas* (including *Copromonas*) are parasites in the intestinal tracts of various animals (8, 29). The general structure is quite like that of other Euglenineae; there is a similar vacuolar apparatus, and paramylon and fat occur as food-reserves.

All the Peranemaceae, however, show dorsiventral organisation, the flagella arising from the ventral surface a little behind the front end (fig. 242 A, G). The individuals most usually show gliding or creeping movements with the ventral surface adjacent to the substratum. During such progression the body may exhibit wave-like contractions, while the single flagellum, or the forwardly directed flagellum of the biflagellate forms, remains rigid, only the apical part showing movements and appearing to function as a tactile organ (74 *a*). The individuals can, however, also swim freely.

In many cases two flagella are present, one directed forwards and the other trailing behind during movement, and according to Lackey (66 *a*) this is also the case in *Peranema*[2] which has usually been described

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[1] See (59), (63), (64) p. 362, (82), (96).

[2] See (3), (19), (36), (51), (52), (54), (66 *a*). Schaeffer's *Jenningsia* (89) is very similar to *Peranema*.

Fig. 242. Astasiaceae and Peranemaceae. A, *Heteronema acus* (Ehrenb.) Stein. B, *Distigma proteus* Ehrenb. C, D, *Heteronema acus*; in C the nucleus shows the first indications of the prophase; D, anterior end enlarged. E, *Astasia Klebsii* Lemm. F, G, *Petalomonas mediocanellata* Stein; F from the ventral surface; G, side-view. H, *Menoidium incurvum* (Fres.) Klebs, individual in optical longitudinal section. I, *Entosiphon sulcatum* (Duj.) Stein. J–L, *Urceolus cyclostomus* (Stein) Mereschk.; J, entire individual; K, periplast in section; L, siphon and vacuolar system. *a*, paramylon; *b*, basal granules; *c*, chromatin; *ce*, centrosome; *co*, connecting-piece of siphon; *e*, endosome (caryosome); *f*, flagellum; *fb*, food-body; *g*, canal (gullet); *k*, caryosome; *l*, caryolymph of nucleus; *m*, mouth; *n*, nucleus; *p*, ribs of periplast; *r*, reservoir; *rh*, rhizoplast; *s*, siphon; *v*, contractile vacuole. (C, D after Loefer; E–G after Klebs; H after Hall; I after Lackey; the rest after Lemmermann.)

as uniflagellate. It is probable that the flagella in all cases arise from the wall of the reservoir, as in *Euglena*. In *Peranema*, whose cells are highly metabolic, there is a slight ventral groove anterior to the opening of the canal which is occupied by the anterior flagellum (51), while in *Heteronema* (69) and *Entosiphon*[1] the aperture of the canal is often oblique (fig. 242 A). *Urceolus* (76) has but a single flagellum arising from a large funnel-shaped depression at the apex (fig. 242 J). Here the periplast is coarsely striated and allows of considerable change of shape, while in *Entosiphon* and the uniflagellate *Scytomonas* it is firmer, in the former bearing prominent longitudinal ribs. In some species of *Heteronema* the body is spirally twisted. A number of genera have flattened cells; examples are *Petalomonas* (64), in which the periplast often bears longitudinal ridges (fig. 242 F) and *Anisonema* (13, 64) which is biflagellate and shows a prominent ventral furrow running practically the whole length of the individual.

The above-mentioned *siphon* is typically developed in *Entosiphon*, *Peranema*, and *Urceolus*, while that of *Heteronema* is smaller; it is lacking, for example, in *Petalomonas* and *Anisonema*. In *Entosiphon* it forms a cone-shaped tube (fig. 242 I, *s*) traversing nearly the whole length of the body, open in front and tapering to a point at the back end. In *Peranema*, *Heteronema* (fig. 242 C, D), and *Urceolus* (fig. 242 L), however, it appears to consist of two longitudinal pieces somewhat widened into an anterior funnel (fig. 242 D, L), where the two rods are sometimes connected, the whole being placed more or less obliquely a short distance behind the anterior end of the individual. In addition there is an arched rod (*co*), extending from the anterior end of the siphon to the surface of the periplast. It appears that the siphon disappears during division and that new ones are formed in the daughter-individuals (12, 65, 88 *a*).

The function of these characteristic structures is scarcely yet clear. They appear in all cases to be movable and can be pushed forwards, as well as from side to side. Only in *Entosiphon* and in *Peranema* (99), however, does the siphon seem to be capable of being slightly protruded from the anterior end of the individual. Movement of the siphon seems to effect a kind of suction whereby particles are caused to stream towards the opening of the canal, and in *Peranema* it has been stated (12, 52) to open and close the cytostome during feeding. There is rather general agreement that ingestion of food takes place through the canal by way of a cytostome located in the reservoir which thus acts as a kind of gullet (49 *a*, 51, 52, 69, 89, 99), although other workers (12, 88 *a*) have stated that the cytostome is related to the siphon and is separate from the reservoir. According to Lackey (65) *Entosiphon* is solely saprophytic, but this is not in accord with other records (cf. (96) p. 178). The undigested

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[1] See (19), (65), (66), (87), (95).

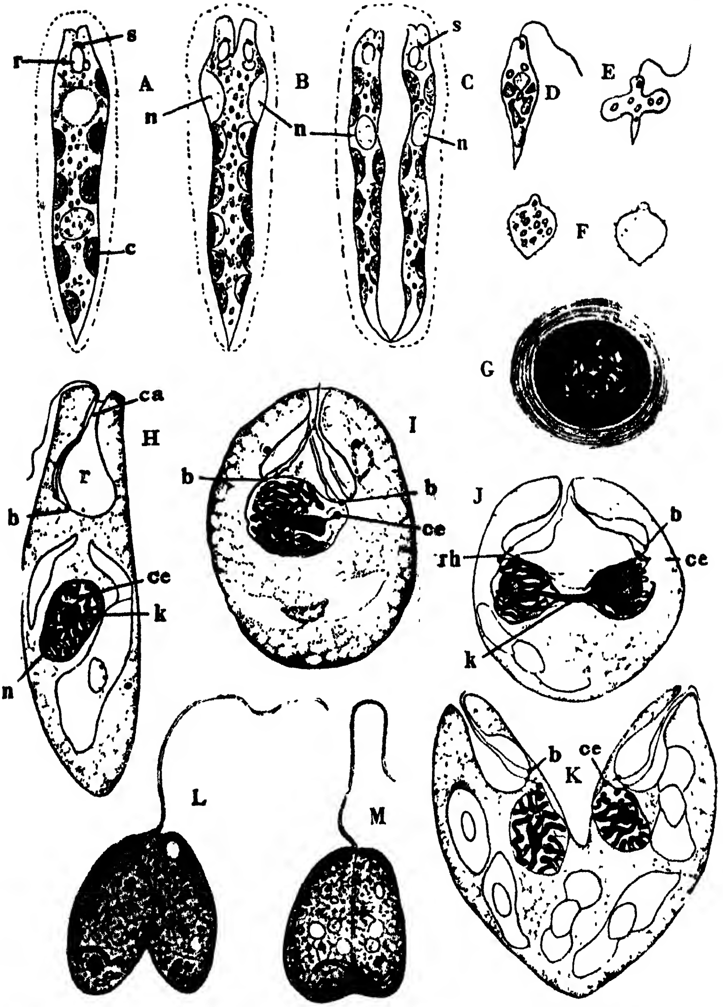

Fig. 243. Reproduction of the Euglenineae. A–C, *Euglena deses* Ehrenb. (after Klebs), three successive stages in division. D–F, *E. chlamydophora* Mainx (after Mainx); D, E, two individuals showing metaboly; F, cysts. G, *E. viridis* Ehrenb. (after Klebs), cyst. H–K, *E. gracilis* Klebs (after Baker), successive stages in division. L, M, *Scytomonas pusilla* Stein (after Dobell), two stages in sexual fusion. *b*, basal granule; *c*, chloroplast; *ca*, canal; *ce*, centrosome; *k*, caryosome; *n*, nucleus; *r*, reservoir; *rh*, rhizoplast; *s*, stigma.

remnants of the food are excreted at a definite point in the posterior part of the body in *Peranema* (3, 66 a).

REPRODUCTION OF THE EUGLENINEAE[1]

Reproduction of the Euglenineae is, as usual in flagellate types, effected mainly by longitudinal division, although Tannreuther (99) records transverse division as an abnormal phenomenon in *Euglena gracilis*. In most cases the individuals come to rest, secrete an envelope of mucilage (fig. 243 A), and then proceed to divide, fission commencing at the front end of the protoplast (fig. 243 B, C). In certain species of *Euglena*, *inter alia*, the cells tend to round off at these times and may then divide again and again to form palmelloid groups, easily distinguishable from the similar stages found in other classes by the presence of paramylon. Sporangial stages, where a number of new individuals are formed within a common envelope, are also known (19, 40).

In *Eutreptia*, *Astasia*, and *Distigma*, however, division takes place during movement. In the encapsuled forms (e.g. *Trachelomonas*) one of the two new individuals usually escapes from the parent-envelope and, after a period of swarming, secretes a new envelope, while the other remains within that of the parent; according to Gimesi (43) there are certain differences in the structure of the nucleus between the retained and the liberated individuals. It seems, however, that in *Trachelomonas* the entire protoplast may also escape from the envelope and only subsequently undergo division (24, 104).

Cysts with a thick firm membrane, composed of an unidentified carbohydrate ((14) p. 203), are commonly formed in *Euglena* (85). Here they are usually spherical, have a thick stratified membrane (fig. 243 G), and contents which are commonly coloured red by haematochrome. In *E. chlamydophora* (73) the cyst-membrane is of a characteristic shape (fig. 243 F). Forms with a rigid periplast (*Lepocinclis*, *Phacus*, *Menoidium*) possess resting stages which quite resemble the ordinary individuals, and the same is the case in *Trachelomonas*. Temporary encystment, on the part of individuals which may or may not retain their flagella, is also recorded in *Euglena* (46, 99); such cysts are surrounded by a delicate mucilage-envelope.

An isogamous sexual process, involving the fusion of amoeboid gametes provided with two chloroplasts, has been recorded by Haase ((47) p. 52) in *Euglena sanguinea*, although this at present awaits confirmation. The zygote is stated to divide without a resting period and to give rise to a number of small vegetative individuals. Dobell (29) described a fusion of ordinary individuals (fig. 243 L, M), preceded

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[1] See especially (4 a), (19), (63), (64), (68).

by nuclear division and abortion of one of the two resulting nuclei of each gamete, in *Scytomonas pusilla* Stein (*Copromonas subtilis* Dobell). Berliner (8) has recorded a similar case in another species of the genus. Recent workers with Euglenineae have failed to obtain any indications of sexual reproduction, and it is noteworthy that in *Entosiphon* and *Peranema* Lackey (66) observed neither conjugation nor encystment during prolonged cultures covering several hundred generations.

AFFINITIES AND CLASSIFICATION OF EUGLENINEAE

The affinities of this specialised class are quite obscure, but it is of interest to note that, in spite of its limited development, parallelism with other classes of Protophyta is displayed in so far as, apart from the motile unicell, we find the encapsuled type and the dendroid colony (*Colacium*). Various authorities (cf. (96) p. 174) have assumed a relationship with Chloromonadineae, with which the biflagellate forms show some resemblance in the arrangement of the flagella and the complex vacuolar apparatus, but such an affinity can at best be only a remote one. The simpler forms discovered by Schiller (p. 732) may ultimately shed more light on the relationships of the class.

It is usual to class the Euglenineae in three families, comprising the holophytic, saprophytic, and holozoic forms respectively and, although this is no doubt artificial,[1] it affords a convenient synopsis.

1. *Euglenaceae:* Amphitropis, Ascoglena, Chlorachne, Colacium, Cryptoglena, Euglena, Eutreptia, Gymnastica, Lepocinclis, Ottonia, Phacus, Trachelomonas.
2. *Astasiaceae:* Astasia, Distigma, Menoidium.
3. *Peranemaceae:* Anisonema, Entosiphon, Heteronema, Peranema, Petalomonas, Scytomonas, Urceolus.

LITERATURE OF EUGLENINEAE

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[1] The Peranemaceae should probably be restricted to the forms possessing a siphon, the other genera being referred to Astasiaceae.

APPENDIX

THE RESIDUAL COLOURLESS FLAGELLATA

The numerous colourless motile forms already considered under the various classes in the preceding pages[1] betray by one feature or another their close affinity to definite pigmented forms. There still remain, however, a large number of similar colourless organisms which in part show considerable specialisation and furnish no evident clues as to their relationships. It is with these that the present section deals. Their ranks have during the present century undergone continual depletion as a better insight into their characteristics and into those of the holophytic forms has exposed affinities with pigmented types (cf. the Monadaceae, dealt with on p. 538), and the question arises whether all of the colourless Flagellata may not ultimately prove to be derived from such an ancestry and to represent forms which have become secondarily colourless. Pascher (48) is of the opinion that this is probably the case, but although many of the forms considered below give the impression of being derivative types, there is no very satisfactory evidence at present to support this view. Nor does there appear to be any good reason for denying the possibility that some series of colourless Flagellata may have been colourless from the first ((18 *a*) p. 141).

Diverse authorities ((49) p. 7) hold that the possession of an eye-spot is indicative of derivation from a pigmented type, the eye-spot being regarded as a modified chromatophore and as the sole persisting relic of the photosynthetic apparatus. This turns on the question of the interpretation of the eye-spot (p. 33), but has probably a measure of truth in it. Yet, in the absence of other distinctive characters the forms with eye-spots must still be left among the colourless Flagellates. Such organisms, however, often retain the characteristic storage-product of their pigmented allies (starch in *Polytoma*, leucosin in Monadaceae, etc.), and this has helped in the elucidation of the affinities of several of them, although the adoption of the colourless habit seems ultimately to lead to the storage of fat (cf. p. 90).

It is noticeable that in most of the forms to be considered below the nuclei have well-marked caryosomes (figs. 244 F; 245 A, D) and that there is very commonly a rhizoplast connecting the basal granules of the flagella to the nucleus or to its caryosome. In these respects they resemble the simpler members of the Volvocales,

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[1] See especially pp. 90, 501, 538, 657, 704, 721, 735.

Chrysomonadineae, etc. Multiplication is effected by longitudinal division (figs. 244 P; 245 K), commonly during movement, while resting stages (cysts) have been observed in only relatively few cases (fig. 244 Q). Sexual reproduction has in the main been recorded among the more specialised types and shows marked peculiarities of its own which it is beyond the scope of this work to consider (see (19), (20), (23), (39), (55), (56)); autogamy is frequent.

Our knowledge of these forms is in great part very imperfect and is at present based almost entirely on the freshwater and parasitic forms, although it is evident that a considerable number of similar types also occur in salt water (21, 29). A considerable number are saprophytes, but many are more or less highly equipped for holozoic nutrition.

Since Senn's day ((60); cf. also (36), (39)) it has been customary to group the colourless Flagellata in three main series,[1] viz.:

Protomastigineae, in which absorption of food-particles in holozoic nutrition takes place at a definitely localised point, often developed as a simple mouth (cytostome), although a number of the forms belonging here are merely saprophytes.

Pantostomatineae (also sometimes known as *Rhizomastigineae*), in which such absorption can take place at any point on the protoplast which is commonly capable of marked change of shape.

Distomatineae, a specialised group of binucleate "double individuals" (cf. p. 15) with symmetrically distributed flagella and, in several forms, two symmetrically placed mouths.

The diverse genera included especially in the first two groups constitute a rather heterogeneous assembly and the classification is scarcely a natural one, nor is there any very sharp limit between the Protomastigineae and Pantostomatineae. It is not proposed to undertake any detailed consideration of these forms here, but merely to indicate their essential characteristics by a brief description of typical examples; further details will be found in the works already cited.

PROTOMASTIGINEAE

This, the largest group of colourless Flagellata, includes organisms with one or two flagella. The periplast is always delicate, although there is usually no marked metaboly except at the posterior end. Many members of this group give the impression of marked specialisation in various directions. A number of families are distinguished, of which the biflagellate Monadaceae are almost certainly all colourless derivatives of the Chrysophyceae (cf. p. 538) and the same is possibly true of some or all of the uniflagellate *Oicomonadaceae* (57) (cf. p. 540).

The individuals of *Oicomonas* (29, 39) live in polluted water, while

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[1] The families are listed on p. 754.

Martin(41) has recorded a species from sick soils. The cells have an emarginate anterior end (fig. 244 L, N), often protruded on the dorsal side, a type of body found in many Chrysomonadineae. *O. ocellata* Scherffel(57) possesses an eye-spot. The flagellum arises from a basal granule which is connected by a rhizoplast with the caryosome of the nucleus. Nutrition is holozoic, food being absorbed only at the anterior end. One species, *O. socialis* Moroff ((45) p. 80), forms colonies in which the cells are united by their protruded posterior extremities; the individuals may, however, also occur as solitary stalked epiphytes (fig. 244 N). The formation of cysts is stated to take place endogenously ((39) p. 321). Sexual reproduction has been reported. It is perhaps significant that the Oicomonadaceae and Monadaceae respectively include the most primitive members among the uni- and biflagellate Protomastigineae, while the other families are clearly specialised in type.

The *Craspedomonadaceae*(10, 16) are uniflagellate epiphytes or colonial planktonic forms, with a delicate periplast, found in relatively pure waters. They are distinguished by the fact that one or two funnel-shaped, collar-like, hyaline outgrowths (*c*) of the protoplast are developed at the anterior end around the base of the flagellum (fig. 244 I, K). These structures aid in the absorption of nutriment. They can undergo change of shape and may at times be altogether withdrawn into the protoplast, to reappear subsequently. Simple forms are represented by the sessile *Monosiga*(29, 63) (fig. 244 I) and the stipitate *Codonosiga*,[1] the stalk of the latter being commonly branched and bearing a number of individuals (fig. 244 Q). In *Astrosiga*(29, 66) and *Sphaeroeca*(34, 36) (fig. 244 G, M) such individuals are united by the stalks to form free-swimming colonies, whose cells in the case of the latter are embedded in mucilage. Another type of colony is seen in *Desmarella*(29, 63), where the stalkless individuals are joined laterally (fig. 244 T).

Diplosiga(18, 66) (fig. 244 K) only differs from *Monosiga* in the possession of two collars. Not uncommon epiphytes are constituted by the species of *Salpingoeca*[2] (fig. 244 J), in which the individuals are provided with a sessile or stalked envelope (*e*) from which the protoplasmic collar (*c*) usually projects; in the otherwise similar *Diplosigopsis*(16) there are two collars. A very remarkable form is *Phalansterium*(11, 61) which is usually placed in a distinct family. Here the individuals are embedded in the apical parts of well-branched coarsely granular mucilage-masses (fig. 244 S). The collar is quite enclosed in the mucilage and in this case seems to have nothing to do with nutrition.

The biflagellate series includes, apart from the Monadaceae

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[1] See (9), (13), (14), (27), (28), (61), (63). The name is also written *Codosiga*.

[2] See (9), (13), (21), (25), (28), (40), (59), (61), (63).

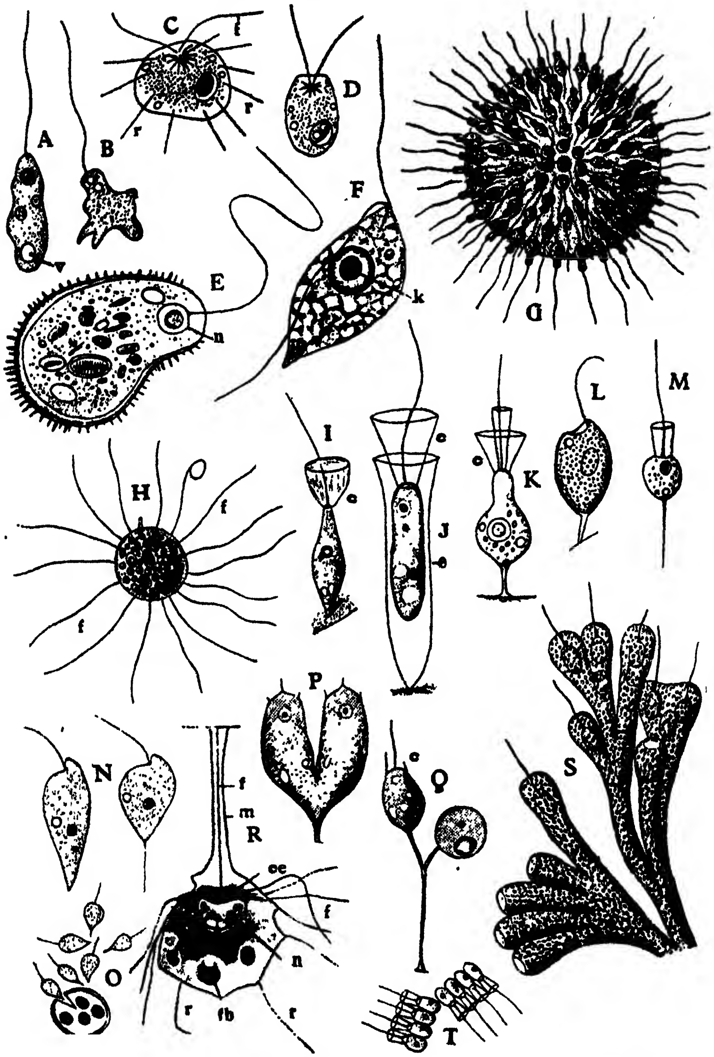

Fig. 244. A, B, *Mastigamoeba invertens* Klebs. C, D, R, *Dimorpha mutans* Gruber; C, rhizopodial and D, flagellata stages; R, attached individual, stained. E, *Mastigamoeba spicata* Penard. F, *Cercobodo crassicauda* Alex. G, M, *Sphaeroeca Volvox* Lauterb.; M, single cell. H, *Multicilia lacustris* Lauterb. I, *Monosiga fusiformis* Kent. J, *Salpingoeca vaginicola* Stein. K, *Diplosiga Francei* Lemm. L, *Oicomonas excavata* Schew. N, *O. socialis*

(p. 538), the *Bodonaceae*, in which the two flagella point in opposite directions during movement (fig. 245 A, B), the backward one sometimes serving for attachment to a substratum (species of *Bodo*). In *Bodo*[1] (fig. 245 A, B) each flagellum arises from a basal granule which is connected by a delicate rhizoplast with a large specially differentiated blepharoplast (cf. below), formed by division from the caryosome of the nucleus. The variously shaped individuals are mostly free swimming and are inhabitants of strongly polluted waters. The anterior end is commonly protruded and pointed (fig. 245 B) and in several species this protrusion is pushed into the prey (other Flagellates, Infusoria) and the nutriment absorbed with its help, although in others the food is engulfed by the anterior end in the usual way.

In the allied genus *Rhynchomonas* (5) (fig. 245 C) the forwardly directed flagellum is replaced by a movable tentacular protrusion of the body which serves to push the food towards the cytostome ((49) p. 13). According to Belar this tentacle contains an axial thread (fig. 245 D, *d*) similar to that constituting the backwardly directed flagellum (*f*), from which it only differs in the very thick cytoplasmic envelope. *Rhynchomonas* normally has two blepharoplasts (*b*), lying one behind the other, the two flagella arising directly from the anterior one, without basal granules. This blepharoplast (sometimes also the other, cf. fig. 245 D) is connected to the nucleus by a thread. *Bodo* and *Rhynchomonas* are the only Protomastigineae possessing these specialised blepharoplasts, apart from the Trypanosomaceae and Cryptobiaceae mentioned below.

Bicoeca,[2] representative of the *Bicoecaceae*, has its cells contained in a wide envelope which is usually attached to a substratum (fig. 245 N). Of the two flagella, one extends freely into the water, while the backwardly directed one (*f*) serves as a contractile stalk fixing the individual to the base of the envelope. The anterior extremity is protruded into a lip-like outgrowth (peristome, *p*) which aids in the absorption of nutriment. In *B. dinobryoides* Lemm. (40) epiphytic colonies are formed just as in *Dinobryon* (p. 529), while in *B. socialis*

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[1] This includes *Prowazekia* (4, 32, 65). See also (6), (13), (14), (24), (40), (45), (56), (59), (61).

[2] See (9), (21), (28), (60–62), (66). This genus was first described as *Bicocoeca*.

Moroff, on the left a free-swimming, on the right an attached individual. O–Q, *Codonosiga Botrytis* (Ehrenb.) Kent; O, liberation of swarmers from cyst; P, division; Q, cyst-formation. S, *Phalansterium digitatum* Stein, part of a colony. T, *Desmarella moniliformis* Kent. *c*, collar; *ce*, centrosome; *e*, envelope; *f*, flagellum; *fb*, food-body; *k*, caryosome; *m*, mucilage-envelope of flagellum (in R); *n*, nucleus; *r*, rhizopodium; *v*, contractile vacuole. (E after Penard; F after Alexeieff; I after Kent; J after Francé; L after Schewiakoff; N after Moroff; O–Q after Fisch; R after Hartmann from Belar; the rest after Lemmermann.)

Lauterborn(34, 36) (fig. 245 E) the individuals are united to form stellate free-swimming colonies.

In the *Amphimonadaceae*(40) the two flagella are equal and both directed forwards (fig. 245 I). The individuals of *Amphimonas* are usually epiphytic, being sometimes situated at the end of a long delicate stalk. A remarkable member of this family, encountered especially in moorland waters, is *Rhipidodendron splendidum* Stein(24, 61). Here the cells are situated within the extremities of long mucilage-tubes joined to form fan-shaped groups.

To the Protomastigineae also belong the highly specialised forms included in the uniflagellate *Trypanosomaceae* and the biflagellate *Cryptobiaceae*, which are in the main parasites in the blood of diverse animals and some species of which are responsible for diverse tropical diseases (sleeping sickness, etc.). In *Trypanosoma* the single flagellum is continued backwards as the thickened edge of an undulating cytoplasmic membrane (*m*) which extends to the posterior end of the flattened individual and aids in movement (fig. 245 H), while in *Cryptobia* (fig. 245 M) the edge of the undulating membrane (*m*) is constituted by the second backwardly directed flagellum which projects freely beyond the posterior end. In these forms, as in *Bodo*, there is a prominent blepharoplast staining with nuclear stains and regarded by some as a second nucleus (kinetonucleus). In *Trypanosoma* (fig. 245 H, *b*) this is situated at the posterior end where it connects with the marginal prolongation of the flagellum.[1]

The Trypanosomaceae also include the genus *Leptomonas*,[2] the species of which are found in the intestines of insects (commonly in the house-fly, see (55), (64)), as well as in the latex of *Euphorbias*, *Ficus*(26 a), and Asclepiadaceae. In the case of the latex-inhabiting forms (fig. 245 J, K) the individuals are so transparent that their presence is difficult to detect until stains are employed(44). According to Lafont(33) the *Euphorbias* attacked by the Flagellate grow poorly, the leaves tend to drop off, and the plants often slowly die. Transference from one plant to another is effected by Hemiptera(15, 17, 26, 42); flies are also suspected.

PANTOSTOMATINEAE

The mainly holozoic Pantostomatineae are common inhabitants of the bottom deposits in waters rich in vegetation, but they are met with also in polluted waters and in old cultures. The principal forms are classed in the *Rhizomastigaceae* of which *Mastigamoeba*[3] (fig. 244

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[1] A further consideration of these forms is impossible here. See Minchin, *Introduction to the Study of the Protozoa*.

[2] Some species are included in the genera *Herpetomonas* and *Phytomonas*, but the prevalent view seems to be that there are no adequate generic differences. For other literature, apart from that cited above, see (2), (3), (7), (38), (46), (47).

[3] See (37), (40), (43), (45), (53), (54), (58), (59), (63).

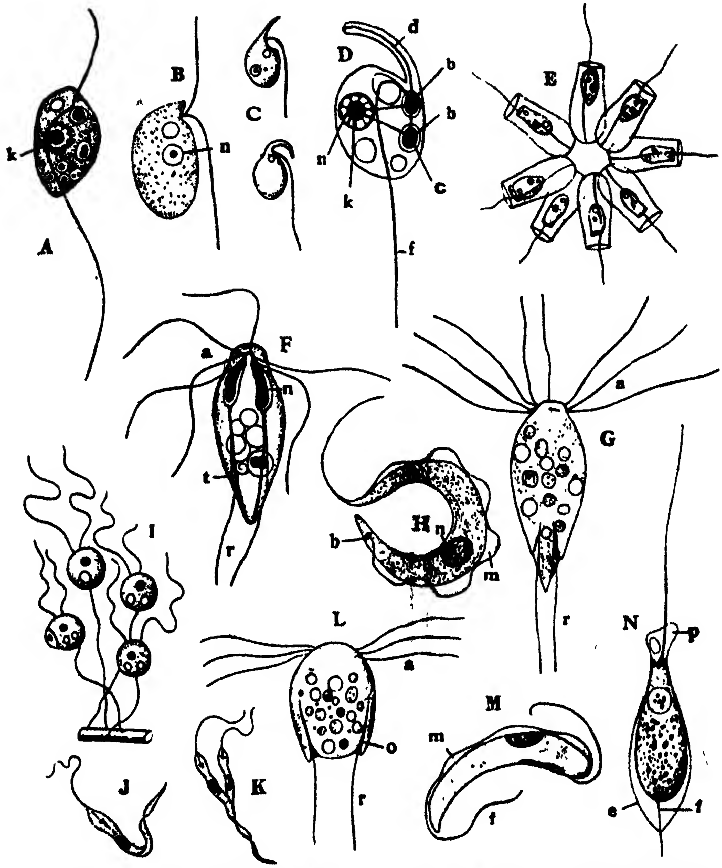

Fig. 245. A, *Bodo minimus* Klebs. B, *B. edax* Klebs. C, D, *Rhynchomonas nasuta* (Stokes) Lemm.; C, two individuals with the tentacle in different positions; D, stained individual. E, *Bicoeca socialis* Lauterb. F, *Hexamitus fissus* Klebs, stained individual. G, *Urophagus rostratus* (Stein) Klebs. H, *Trypanosoma damoniae* Lav. et Mesnil, stained individual. I, *Amphimonas globosa* Kent. J, K, *Leptomonas Davidi* Lafont; K, a dividing individual. L, *Hexamitus inflatus* Duj. M, *Cryptobia Borreli* (Lav. et Mesnil) Lemm., stained individual. N, *Bicoeca lacustris* J. Clark. *a*, anterior flagella; *b*, blepharoplast; *c*, central body of blepharoplast (in D); *d*, axial thread of tentacle (in D); *e*, envelope; *f*, flagellum; *k*, caryosome; *m*, undulating membrane; *n*, nucleus; *o*, oral fissure; *p*, peristome; *r*, posterior flagella; *t*, rod of firmer substance. (A, F after Alexeieff; B, G after Klebs; D after Belar; H, M after Laveran and Mesnil; J, K after Lafont; the rest after Lemmermann.)

A, B, E) and the allied *Mastigella* (19, 40) afford typical examples. These are amoeba-like organisms, with an ill-defined or well-marked (fig. 244 E) periplast, but provided with a rigid flagellum which is often several times the length of the body. In *Mastigamoeba* it can be traced up to the nucleus where it terminates in a granule (fig. 244 E), while in *Mastigella* there is no such connection with the nucleus.

The individuals can swim freely with the help of the flagellum, but commonly creep over the substratum in an amoeboid manner, although retaining the flagellum which is suspected of serving as a tactile organ. Most species are holozoic, the food being absorbed by means of pseudopodia arising at any point on the body, although in a few cases confined to the posterior end. At times so large a quantity of Algae may be taken up as to cause the cells to appear green or brown. There is commonly only a single contractile vacuole, situated at the front or the back end (fig. 244 A, *v*). Several species show a peculiar development in the shape of a mulberry-like appendage at the back end. Multiplication is effected by longitudinal division during movement or after the organism has come to rest. The accounts of sexual reproduction are not very convincing (see (19)).

Gruber's *Dimorpha* (8, 22, 50) (fig. 244 C) differs in possessing two equal flagella (*f*) and in the fact that the body bears a number of delicate radiating rhizopodia (*r*), each provided with an axial fibre. These fibres (fig. 244 R, *r*) radiate outwards from a centrosome (*ce*) lodged in a concavity of the nucleus and from which the two flagella (*f*) also arise ((6 *a*) p. 32). At times the rhizopodia can be completely withdrawn (fig. 244 D) and the ovoid cell swims freely with the help of its flagella, one of which is then directed forwards, while the other trails behind. The organism can also attach itself to a substratum (6 *a*) by means of the forwardly directed flagellum (fig. 244 R) which then develops a mucilage-envelope (*m*). Small organisms which come into contact with the rhizopodia are stated to be killed ((22) p. 450) and then glide along them to the surface of the protoplast, there to be enveloped by pseudopodia. This form shows much resemblance to some of the Heliozoa except for the persistent nature of the flagella.

The orientation of the flagella is the same in *Cercobodo*[1] (fig. 244 F), the individuals of which can at times assume an amoeboid form so as to resemble a biflagellate *Mastigamoeba*. The flagella arise from a basal granule connected by a double rhizoplast with the nucleus. Cysts with a firm membrane have been recorded in certain species.

To the Rhizomastigaceae are also referred the epiphytic *Pteridomonas* (50) and *Actinomonas* (21, 63), found in pure stagnant waters. Both possess numerous rhizopodia and a single flagellum and are attached by a long delicate stalk to the substratum. *Pteridomonas*, which has

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[1] This includes *Dimastigamoeba* (45), as well as certain species formerly referred to *Cercomonas*. See also (31), (43), (54), (59).

also been found swimming freely, has the rhizopodia arranged around the base of the flagellum and thus shows much resemblance to some of the Cyrtophoraceae (Chrysophyceae, p. 532).

The remarkable *Multicilia*(12, 35, 52), a form inhabiting sediments, is usually referred to a separate family (*Holomastigaceae*). In *M. lacustris* (fig. 244 H) a considerable number of flagella (*f*), each arising from a separate basal granule, are evenly distributed over the surface of the slightly amoeboid protoplast, whilst in *M. palustris*(51) the organism is polyhedral with the flagella arising at the corners. There are numerous peripheral contractile vacuoles and often several nuclei with prominent caryosomes. Multiplication takes place by division during movement. This organism is generally regarded as primitive, but there do not appear to be any very good reasons for this view.

DISTOMATINEAE(24, 30)

This highly specialised group of binucleate double individuals includes only relatively few forms placed in the single family *Distomataceae*. All have a delicate periplast and show metaboly. They are characteristic of polluted waters where they feed on the bacterial population, while *Octomitus* and some species of *Urophagus* occur in the intestines of fish, frogs, etc.

The double nature of the individuals is plainly evident in *Hexamitus* (9, 59, 61, 63) where the body consists of two symmetrical halves (fig. 245 F, L), each with three anterior flagella (*a*), the two sets arising on either side of the bluntly rounded front end; in addition there is a backwardly directed flagellum (*r*) on each half, so that there are eight flagella in all. Each flagellum arises from a basal granule which is connected with its appropriate nucleus (*n*), as well as with the other basal granules (fig. 245 F). The two nuclei (*n*), each with a prominent caryosome, possess an elongate shape and are located near the anterior end. A pair of oral fissures (fig. 245 L, *o*) are symmetrically placed on either side of the body and from these fissures the backwardly directed flagella (*r*) usually arise. The apertures of the fissures can be widened and narrowed, the movements of the associated flagella serving to waft food-particles into them. Running from each nucleus to the posterior end of the body is a rod of firmer substance (fig. 245 F, *t*) whose function is unknown, although it has been suspected of being mechanical. Highly refractive globules occurring in the protoplast seem to consist of a substance resembling glycogen; there is also the usual fat.

A very similar form is *Urophagus*(1, 45) which, however, lacks the oral fissures, nutriment being absorbed with the help of a bivalved posterior prolongation, the valves of which can separate and approximate (fig. 245 G). *Octomitus*[1] (56) likewise lacks the oral fissures.

INTERRELATIONSHIPS AND AFFINITIES OF THE COLOURLESS FLAGELLATA

Lemmermann ((40 a) p. 52; cf. also (60) p. 112) was of the opinion that the uni- and biflagellate Protomastigineae were descended from similar forms among the Pantostomatineae, but for this view it is difficult to find any adequate support. On the contrary, in view of the now practically established derivation of amoeboid and rhizopodial forms from flagellate types in the holophytic classes of Protophyta (see especially pp. 499, 532), it seems much more likely that the Protomastigineae are the more primitive of the two groups. Among them, as already pointed out above, the Monadaceae and Oicomonadaceae appear as relatively unspecialised forms, particularly in such genera as *Monas* and *Oicomonas*. Since there is very little doubt that the Monadaceae represent colourless Chrysomonadineae (p. 538), while a similar relation is suspected for some at least of the Oicomonadaceae, this directs attention to the Chrysophyceae as the possible source of the Protomastigineae. In this connection it is noteworthy that among the members of the latter we have the same three types of flagellar apparatus (Oicomonadaceae, Monadaceae, Amphimonadaceae) as occur in Chrysophyceae. It is therefore not beyond the realms of probability that future research will show that all the Protomastigineae are to be regarded as secondarily colourless Chrysophyceae. As regards the Distomatineae, which are clearly very specialised, it is significant that analogous "double individuals" are known elsewhere at present only among the Chrysophyceae (cf. p. 15).[2]

In the following epitome of the classification of colourless Flagellata only a list of families is given, arranged in a somewhat different sequence to that followed in the foregoing matter and expressing the point of view just put forward:

1. *Monadaceae* (see p. 538).
2. *Oicomonadaceae:* Oicomonas.
3. *Rhizomastigaceae:* Actinomonas, Cercobodo, Dimorpha, Mastigamoeba, Mastigella, Pteridomonas.
4. *Holomastigaceae:* Multicilia.

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[1] According to Hartmann ((23) p. 302) *Lamblia*, which Senn ((60) p. 151) places as a synonym of *Megastoma* (20), is the sexual phase of *Octomitus intestinalis*.

[2] It should, however, be recalled that the colourless Flagellata certainly include a number of heterogeneous forms that may have other affinities (cf. *Furcilla*, p. 90; *Phyllomitus*, p. 657).

5. *Craspedomonadaceae:* Astrosiga, Codonosiga, Desmarella, Diplosiga, Diplosigopsis, Monosiga, Phalansterium, Salpingoeca, Sphaeroeca.
6. *Bodonaceae:* Bodo, Rhynchomonas.
7. *Bicoecaceae:* Bicoeca.
8. *Amphimonadaceae:* Amphimonas, Rhipidodendron.
9. *Trypanosomaceae:* Leptomonas, Trypanosoma.
10. *Cryptobiaceae:* Cryptobia.
11. *Distomataceae:* Hexamitus, Octomitus, Urophagus.

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